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IMPRIMERIE A/S L. IHRICH

On the Importance of Quantitative Investigation of the Bottom Fauna in Marine Biology.

By

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SINCE C. G. Joh. Petersen in 1911 published his first paper on the valuation of the sea, a series of papers on this subject has appeared, and several regions have been studied by means of Petersen's grab. It might therefore be of some interest now to try to summarize all these investigations and to state some general results.

The intention of Petersen, when he started his quantitative investigations on the bottom fauna, was to determine the productivity, i. e. the amount and variation of fish-food and other living animals per sq. m. of sea-bottom, and he further intended to find out an easy method for describing the bottom fauna. But it has turned out that the investigations inaugurated by Petersen have also been of considerable importance to marine zoogeography and ecology.

We shall now begin with the first of the four subjects mentioned above, namely, the productivity of the sea-bottom. I shall here refer to Table I, in which the average weight and number of living animals per sq. m. in the various waters investigated are given. It is obvious that there is a great variation between the different kinds of seas studied, and it should further be pointed out that these variations in the quantity of animals living on the bottom follow certain lines. Among the seas studied, we find the smallest weight, 10—35 g. per sq. m., in the Mediterranean, in the White Sea and in the East Greenland fjords, i. e., waters separated from the ocean by a threshold, and to which there is probably a very poor supply of nitrates and phosphates owing to the dry climate and the low precipitation. In the East Greenland waters the paucity of the animal life is also due to the slight transparency of the water, which again limits the photosynthesis. As was to be expected, we are able to state that in seas in which the conditions for production of organic matter are bad, the quantity of

Table I.

Average number and weight of living animals per sq. m. in various seas.

Name of the sea	Number per sq. m.	Weight in g. per sq. m.
Off W.coast of Italy (9—1030 m.), Spärck, 1929	About 50	About 6
Bay of Algiers (13—400 m.), Spärck, 1929 ..	„ 100	„ 20
Gulf of Rovigno (no records of depths), Vatova, 1934		„ 140
Canal di Leme (about 10—30 m.), Vatova, 1931		„ 50
Off Faro, Portugal (32—95 m.), Spärck, 1929	„ 200	„ 265
Kattegat (about 20 m.), Petersen, 1918	„ 400	„ 250
Off the Faroes (20—270 m.), Spärck, 1929 ..	„ 35	„ 30
Faxe Bay (26—50 m.), Spärck, 1929	„ 300	„ 350
White Sea (0—250 m.), Zenkewitsch, 1927		„ 20
Barents Sea (0—400 m.), Zenkewitsch, 1927, Idelson, 1934		„ 150
Franz Joseph Fjord (0—780 m.), Thorson, 1933, Spärck, 1933		„ 35
Scoresby Sound (0—400 m.), Thorson, 1934		„ 50

Table II.

Showing the number and weight per sq. m in some shallow water areas.

Name of the water	Number of animals	Weight in g. per sq. m.
Laguna Veneta, Vatova, 1931		About 200
Zuider Sea (only mollusca), Havinga, 1922..	About 60	„ 150
Limfjord, Petersen and Boysen Jensen, 1911	„ 400	„ 700
Shallow water of Franz Joseph Fjord (0—45 m.) Thorson 1933	„ 150	„ 100

Table III.

Showing the percentage of the dominant species in some communities.

Name of the animal	Percentage of total number of living animals	Percentage of total weight of living animals
Foraminifera in the *Foraminifera* community in Franz Joseph Fjord	About 99 %	About 50 %
Macoma calcaria in the *Macoma calcaria* community in Iceland.....	„ 50 %	„ 50 %
Spisula solida var. *elliptica* in the *Venus gallina* community in Iceland	„ 50 %	„ 25 %
Modiola modiolus in the *Modiola* epifauna in the Faroes	„ 75 %	99.9 %

bottom animals, and consequently of fish food, is also small, as the figures from the Mediterranean and the East Greenland waters clearly show. If the samples from these waters are studied more in detail (Table II), there seems to be a very close relation between the quantity of bottom animals and the above mentioned conditions for production. Thus the number of animals per sq. m. decreases in the Mediterranean from Gibraltar to the east, and in the East Greenland waters from the open sea towards the inner parts of the fjord systems. The waters hitherto investigated quantitatively which show the poorest bottom fauna are consequently the Gulfs of Naples and Salerno, and the inner parts of the huge East Greenland fjords, Scoresby Sound and the Franz Joseph Fjord, deep waters with a low production of organic matter, caused by various hydrographic and climatological factors. It is in good agreement with this fact that just these waters, both the eastern Mediterranean and the East Greenland fjords, have a fairly insignificant population of bottom fishes.

On the other hand, it can be seen from Table I that the waters in which the greatest numbers of living animals per sq. m. have been found are rather shallow with a considerable water renewal and are surrounded by regions with an Atlantic climate and high precipitation. In the Limfjord and other estuarine waters of similar character we find from Table II that the number and weight of the bottom animals are much higher than in the deeper waters of the same regions. And it further appears from this table that there is a relation between the shallow water of the Mediterranean, north-western Europe and the East Greenland fjords similar to that mentioned above. The lagoon at Venice shows much lower figures than, for instance, the Limfjord, but much higher figures than the Gulfs of Salerno and Naples and the other deeper and open parts of the Mediterranean which have been investigated by these methods. We also observe from Table I a similar difference between the Faxe Bay on one side and the waters round the Faroes on the other. In the latter waters we find a much lower number of animals per sq. m. which is probably due to the low run-off from the land to the sea round these small isolated islands.

We can summarize the above remarks as follows: Though there is only a small number of bottom samples available from most of the waters investigated (from Danish waters several thousand samples covering a period of more than twenty years are at hand), the differences in the quantity, i. e. the number and weight per sq. m., of living animals are very pronounced. These differences, further, are regional, agree quite well with climatological and hydrographical factors, and correspond with the depths and other conditions that influence the productivity of the waters. They must be regarded as a reality. The first and most essential result of this method and these investigations is consequently that we are enabled to establish the productivity of bottom animals of a certain water. As it is a fairly simple task to take 50—70 bottom samples, we have now an easy method by means of which it is possible, from a short cruise, to form

an idea of the amount and production of fish-food in a certain water, and consequently of the fishing possibilities as regards the bottom fishes[1]).

If such investigations be continued for several years, as has been the case in some Danish waters, they enable us to learn the seasonal variations and the variation from year to year. I may here refer to the papers of Boysen Jensen and Blegvad. Again it is possible to reach some general broad results. For the Limfjord, for instance, which is an entirely estuarine water with its own production of plankton, with a hydrography and productive conditions quite independent of the open sea, very considerable quantitative and qualitative variations have been found. On the other hand it is obvious from the above papers by Blegvad that the variations in the Kattegat and the waters round Funen are much less pronounced. These results are not only of interest to fishery biology, but are also of some importance to marine ecology, and it is to be hoped that similar investigations will be undertaken in other seas too. The above-mentioned results allow also the conclusion to be drawn that in deep waters and in the open sea there will be very slight variations in the composition of the bottom fauna, quantitatively and qualitatively, from year to year.

As mentioned above, a further intention of Petersen was to make it possible to give an easy description of the bottom fauna. In this he was influenced by the contemporary plant-ecologists, and he endeavoured to give a short characteristic name to the fauna of a region, just as a few words may give us an idea of the flora of a territory such as a heath, an oak forest, a pine forest, etc. I cannot but say that this intention was realized. Another result of the quantitative bottom investigation is that only a few species are really common, i. e., occur in a considerable number per sq. m. Table III shows that in several areas investigated a single species constitutes more than 50 per cent. of the total weight and number of living animals. In a forest a few species of trees are quantitatively predominant, i. e. not in number per sq. m., but in weight. For such an area with a few quantitatively dominant species Petersen used the word "community". It should be borne in mind that community in the sense of Petersen is used to give a simple and not a detailed description of the fauna, and Petersen does not use this word to describe any ecological unit, biocoenose, etc.

The use of the term "community" has been subject to certain criticism, and the problem whether the communities really "exist" in nature has been discussed. The present author thinks that the adverse criticism is chiefly due to the fact that several investigators consider to too great an extent only the fauna of the single region or sea which

[1]) It will then be possible to prepare a chart of the density of the animals on the sea-bottom, the biomass, and to draw curves (isobenthes) through points with the same density, as has been done by Russian authors (Zenkewitsch, Brotzky and Idelson 1928, Idelson 1934).

they have personally investigated. The use of the term"community" should simply be to give a general, comparative, faunistic description of fairly large areas. It is therefore necessary to *compare* the results obtained from the several waters examined, and it will depend on this comparison to what degree the community method should be used for the description of marine fauna. Stephen is quite right (1934 p. 784) when he points out that most authors feel it necessary to describe new communities. But this is in contradiction to the intention of the method. If it is not possible to state and describe a few communities in the seas, the method is of only slight descriptive value. As Petersen was the first to describe the communities, he had only little opportunity for making comparisons, and it is therefore not surprising if some of the communities of Petersen have to be revised a little. In the following I shall try to give a short synopsis of the communities based on a comparison of the results obtained in the different waters investigated.

It must be remembered, however, that a very important result of the quantitative method is the recognition of the sharp difference between the epifauna and the fauna of the level bottom, the infauna, which has been pointed out by Petersen. Everywhere this difference has appeared very clearly, and it must always be remembered when the fauna of a certain area is to be described that these two parts of the marine bottom-fauna must be described separately. Later on these terms (Endobiosis, Hypobiosis and Epibiosis) have been amplified by Gislén (1931).

A. Level sea-bottom.

1. Shallow water communities, i. e. communities of which the upper limits are the beach.

(a) *Macoma calcaria* community. This community is characterized by the occurrence of *Macoma calcaria* as the constantly predominating species. Besides this species various species of *Astarte (borealis, elliptica, montagui), Portlandia, Yoldia hyperborea, Nucula tenuis, Leda* etc. may occur; also *Nephthys ciliata,* species of *Pectinaria* and *Harmothoë, Onuphis conchylega,* and several other Polychæta have been found. Among Echinoderms *Myriotrochus rinki* and *Ophiocten sericeum* are the most frequent. The Ostracoda *Philomedes globosus* may also be mentioned. This community has been described from the coasts of the East Greenland fjords (Thorson 1933, 1934, Spärck 1933), where it seems to occur everywhere on clay bottoms and on sand mixed with clay. It occurs in different locally and bathymetrically determined varieties. The lower limit of this community in the East Greenland fjords is about 50 m. Outside the East Greenland fjords this community has been described from various other arctic waters, namely the Storfjord in Spitzbergen (Brotzky 1931), where this community is present in the inner part of the fjord, on soft bottoms near the Spitzbergen Bank (Idelson 1931), in the waters near the Kanin Peninsula (Zenkewitsch 1931) in parts of the Barents Sea, in the White Sea

(Zenkewitsch 1927) and Northern Norway (Soot-Ryen 1924). In the Barents Sea it occurs at greater depths than in the East Greenland waters, down to 100—150 m. Outside the arctic waters the *Macoma calcaria* community occurs at Iceland and the Faroes (Spärck 1929), but here — at least at the Faroes and south and west Iceland — only at the heads of the bays and fjords, and it has also been mentioned as occurring in some Scandinavian fjords, the southern Baltic and in the Belt Sea (Petersen, Broch 1927). The occurrence of these mainly arctic communities in the inner part of fjords in more southerly regions and in the Baltic may perhaps be considered to be of the nature of a survival. The amount of living animals in this community is rather variable; in pure arctic waters the weight of living animals per sq. m. is about 100—200 gm., in the Faxe Bay for instance on several stations 400—500 gm. or more. As a whole it is fairly highly productive for a shallow water community.

(b) *Macoma baltica* community. This community is characterized by the occurrence of *Macoma baltica.* In addition *Cardium edule, Mya arenaria, Arenicola marina,* and, locally, *Scrobicularia plana* are the most abundant. This community occurs in north-western Europe in shallow water, i. e. only down to a few metres. In the Baltic, where it is the only marine community in the inner parts, it occurs at much more considerable depths. Here the *Macoma baltica* community and the *Macoma calcaria* community are interwoven to a certain extent. But apart from the Baltic these two communities are very distinct. The *Macoma baltica* community is found in a single isolated locality in the White Sea (Zenkewitsch 1927), but it does not occur at all at Iceland and the Faroes. Further, it is described from Scotland (Stephen 1929), the east coast of England (Blegvad 1922), the north-west coast of Germany (Hagmeier 1923), the Zuider Sea (Havinga 1922), the Oslo Fjord and on all the Danish and most Scandinavian coasts, except the west coast of Jutland (Petersen, Soot-Ryen 1924), the Baltic (Petersen, Thulin 1922, Hessle 1923 and 24, Segerstråle 1933). As no data from investigations of this kind are at hand from south-west Europe nothing definite can be said as to how far south this community occurs, but it seems to be of very little importance south of the English Channel. The *Macoma baltica* community thus seems to occur along the coasts of the European continent and the British Isles at least as far south as the English Channel, and it penetrates into the inner Baltic, though here it is mixed with brackish-water animals. It occurs on soft and sandy bottoms, when the sand is not quite pure and not too hard. It is not found on rocky coasts or coasts with a violent surf. This community must be regarded as corresponding to the *Macoma calcaria* community of the more northern waters.

(c) *Macoma nasuta* community. According to Shelford and Towler (1925) a community characterized by *Macoma nasuta* and other *Macoma* species occurs on the coast at Puget Sound in shallow water. In addition *Cardium corbis* and *Arenicola claparedei* and several

other Lamellibranchs and Polychæta are described from this community, which in the north-western Pacific seems to correspond to the above mentioned *Macoma baltica* community of north-western Europe. Also in Japan, a *Macoma* community of this kind seems to occur (Gislén 1931).

(d) *Tellina tenuis* community. This community is characterized by the occurrence of *Tellina tenuis*, and of *Donax vittatus*, *Nephthys coeca* and other Polychæta. The number of species in this community seems to be much smaller than in the foregoing ones, and this is doubtless due to the rather specialised conditions under which the components of this community live. The *Tellina tenuis* community occurs on pure sandy bottoms, i. e. on coasts with a fairly heavy surf. This may be considered the reason why only comparatively few species live in this community and why it is only of little interest to fishery biology. It is described especially from the Scottish coasts (Stephen 1929), but occurs along the west coast of Jutland too, and it may be supposed to occur in other similar localities in western Europe.

(e) *Tapes aureus* community. A community in the lagoon of Venice dominated by *Tapes aureus* has been described (Vatova 1931), in it *Ensis siliqua*, *Corbula gibba*, *Nucula nucleus*, *Loripes lacteus*, and other Lamellibranchs occur. Among Polychæta *Eunice vittata*, *Glycera*, *Nephthys hombergi* and others are recorded. This indicates, among other things, that in the Mediterranean and presumably also in south-western Europe we meet shallow water communities characterized by *Tapes*, *Loripes*, *Scrobicularia* etc. No quantitative details are available from these districts, however.

From the above it is evident that there are at least 3 to 4 shallow water communities in western Europe, one succeeding the other from the north to the south, characterized by Lamellibranchs, especially by the *Macoma* and *Tellina* species, and Annelids.

2. Communities of waters of medium depths, i. e. the communities of the shelf outside the shallow water communities.

(a) *Astarte crenata* community. This community is characterized by *Astarte crenata*, by *Arca glacialis* and also by several of the Lamellibranchs and Annelids which were also found in the *Macoma calcaria* community, several species of *Portlandia*, *Cardium*, *Pecten groenlandicus* for instance. The number of species and individuals are, however, much lower than in the *Macoma calcaria* community. This community is described from East Greenland waters, inside the fjords and also in the pack-ice belt at depths from about 50 m. to about 250 m. (Spärck 1933, Thorson 1934). Further, according to the papers by Zenkewitsch, Brotzky and Idelson it seems to occur in the central parts of the Barents Sea and in the Kara Sea, and it therefore appears to occur in arctic seas — in several varieties below the *Macoma calcaria* community. It seems also to occur in Ramfjord in northern Norway (Soot-Ryen 1924). It occurs on a bottom which consists more or less of clay. In most cases the weight per sq. m. in this community is less than 50 gm.

(b) *Amphiura* community. In most waters in north-western Europe on soft bottom areas outside the shallow water community we find a community characterized by *Amphiura filiformis* or *Amphiura chiajei, Turritella communis* and *Aporrhais pes pelecani, Thyasira flexuosa, Syndosmya nitida, Brissopsis lyrifera, Echinocardium cordatum* and various Polychæta occur in this community. This community ranges from south Iceland and the Faroes (Spärck 1929), where a variety occurs with *Thyasira* predominating, the Scottish waters (Stephen), the southern North Sea (Blegvad 1922, Davis 1925, Hagmeier 1923), Kattegat, Skagerak and the Sound (Petersen, Blegvad), the Gullmar Fjord (Molander 1927) through the English Channel (Ford 1923) to the Mediterranean (Spärck 1931, Vatova 1931 a). This community predominates consequently along the coasts of north-western and western Europe and in the Mediterranean on clay and mixed bottoms from about 15—20 m. down to about 100 m., i. e., the inner part of the shelf. In some waters, where the food conditions are good, the amount per sq. m. in this community may be considerable, e. g., in the Kattegat and the southern North Sea, where it may be several hundred gm. In the Mediterranean and at the Faroes it is lower.

The above mentioned communities seem to be most often distributed on soft bottoms in the northerly and southerly waters of Europe respectively. But there are also a few others, differing so much from the two mentioned above that they must be considered separate communities.

(c) *Syndosmya alba* community. Characterized especially by the occurrence of *Syndosmya alba. Corbula gibba, Cultellus pellucidus, Nucula nitida,* several species of *Nephthys* also occur in this community, which seems to have a fairly restricted range; it occurs in some Danish waters, especially round Funen, in the Sound, in the Issefjord, and in the Limfjord (Petersen, Boysen Jensen, Spärck and Lieberkind, Blegvad), also in the North Sea (Blegvad 1922, Hagmeier 1923, Davis 1924) and in the Channel (Ford 1923), but it is always found in fairly restricted areas with soft bottoms between about 5 and 15 m. The range of the *Syndosmya alba* community seems to a certain degree to coincide with the range of the *Macoma baltica* community, and in certain north west European waters it is found outside the last named community. As it occurs in shallow and protected waters of an estuarine character, it has a rich production, and it is consequently among the communities in which the richest fauna is found.

(d) *Haploops tubicola* community. This is a sharply defined community hitherto only found on clay bottoms in the south-eastern part of the Kattegat, between Anholt, Sealand and the Swedish coast, characterized by hundreds of the tube-building Amphipod, *Haploops tubicola,* per sq. m. *Pecten septemradiatus, Lima loscombi* and *Eumenia crassa* also occur in fairly large quantities.

We shall now consider the communities on hard and sandy bottoms which differ to some extent from the communities on soft bottoms.

(e) *Venus fluctuosa* community. This community is only recorded from Scoresby Sound in East Greenland, but it must be remembered that this is the only really arctic locality where a pure sand bottom has been found over large areas. It reminds us somewhat of the *Macoma calcaria* community but *Macoma calcaria* is replaced by the arctic *Venus* species, *V. fluctuosa* (Thorson 1934). *Astarte borealis, elliptica, montagui* and several other of the common arctic Lamellibranchs and Polychæta occur in the community. The *Venus fluctuosa* community is found at depths of about 10—20 m. The weight per sq. m. of living animals is considerable, though much less than in the corresponding communities in southern seas.

(f) *Venus gallina* community. The *Venus gallina* community is characterized by the occurrence of *Venus gallina* and *V. ovata,* and by *Spisula* — in northern regions *Sp. solida* var. *elliptica,* in the southern regions by *Sp. subtruncata* — *Psammobia teilinella* and several other Lamellibranchs. Among Echinoderms a number of *Spatangidæ (Echinocardium cordatum, flavescens, pennatifidum, Spatangus purpureus)* belong to this community. The *Venus gallina* community is recorded from Iceland, the Faroes (Spärck 1929) and Scotland (Stephen 1922, 1933) where *Spisula solida* var. *elliptica* is predominant, from the Dogger Bank and the southern North Sea (Blegvad 1922, Davis 1923), where *Sp. subtruncata* predominates, Danish waters (Petersen, Blegvad) and the English Channel (Ford 1923), the coast of Portugal, and probably also the Mediterranean (Spärck 1931, Vatova 1931). The *Venus gallina* community occurs on more or less sandy bottoms below the shallow water or coastal communities down to about 100 m. It seems to have the same distribution as the *Amphiura* community, so that the *Venus gallina* community and the *Amphiura* community may be considered as corresponding communities on soft and hard bottoms respectively. The productivity of this community is variable; in some places, the Dogger Bank and Faxe Bay, for instance, it contains a very large amount of living animals per sq. m.

As was the case in the soft bottom communities there are also some sand bottom communities of a more limited range.

(g) *Tellina fabula* community. This community is especially characterized by *Tellina fabula. Nucula nitida* is also fairly common. This community, which is described by Stephen (1923, 1933), may be a community corresponding to the *Syndosmya alba* community as a coastal community on a sand bottom, but it has not been much investigated.

(h) *Venus fasciata* community. This community is characterized by *Venus fasciata,* and by *Glycimeris glycimeris* and *Astarte triangularis.* It occurs on shell gravel and is described mainly from English waters (Ford 1923, Smith 1932); it also seems to occur on the Faroe Bank. It must be regarded as of little importance to fishery biology.

(i) *Venus verrucosa* community. This community characterized mainly by *Venus verrucosa* is described from the Mediterranean by Vatova (1934). It occurs on sandy bottoms.

As will be seen from the above it is obvious that on sand bottoms we have communities which exactly correspond to the soft-bottom communities. One is widely distributed, the *Venus gallina* community, one arctic and several southern ones are of a more limited range.

3. Communities from deeper waters, i. e. the deeper parts of the shelf and the waters outside.

From really deep water, i. e. more than a hundred metres, only very few bottom-samples are at hand, and as the opportunity for comparison is only small, it is rather difficult to describe communities from deep waters. One or two fairly well characterized communities may be noticed.

(a) *Foraminifera* community. This community is characterized by the dominance of various *Foraminifera*, for instance *Rhabdamina cornuta* in arctic seas, *Psammosphæra fusca* and *Astrorhiza arenaria* in Scottish waters, where this community was described for the first time by Stephen (1923) from depths slightly exceeding 100 m. Further, a very pronounced *Foraminifera* community has been described from 500—700 m. depth in the East Greenland waters, inside as well as outside the fjords (Spärck 1933, Thorson 1934). It is to be supposed that such *Foraminifera* communities will appear to be common in the deeper parts of the sea, and they will probably be found to have a wide distribution. Apart from *Foraminifera* the other animals are few, some Annelids and Mollusca, the former predominating.

(b) *Pecten vitreus* community. In the Skagerak at depths below 200 m. a community characterized by the occurrence of *Pecten vitreus* is described by Petersen (1916). *Malletia obtusa, Portlandia lucida* and the ubiquitous *Syndosmya nitida* also occur, and among the Echinoderms the Ophiurid *Amphilepis norvegica* is characteristic of this community. The *Ophiura sarsi, Brissopsis lyrifera* and *Amphiura chiajei* community of Petersen seem to represent the transition from the *Amphiura* community to the *Pecten vitreus* community. The *Pecten vitreus* community is not described from waters other than the Skagerak and the deeper parts of the Oslo Fjord, but apart from the above-mentioned East Greenland waters, only very few quantitative samples of the bottom fauna seem to have been taken outside the Skagerak from depths exceeding 200—300 m. From the Mediterranean 5 or 6 samples from depths between 500—1000 m. are at hand, but as they contain practically nothing living they are of no use in this respect.

Consequently, for the present, it is only possible to describe the two above-mentioned communities, the widely distributed *Foraminifera* community and the *Pecten vitreus* community from the Skagerak. As was to be expected, the amount of living animals per sq. m. in these deeper communities is only small, 5—30 gm. per sq. m.

B. Epifauna.

We shall now turn to the epifauna, the animals which live attached to the vegetation, rocks, stones, etc. It is obvious that the collection of samples by means of Petersen's grab in such cases is of much less value than on the level bottom, and that the quantitative results cannot be of any great exactness. Nevertheless, it is possible to obtain minimal numbers, and it may also be possible to obtain sufficient data for a description of some communities in southern seas.

In two papers by Gislén (1930, 1931) the division of the different kinds of epifaunas (epibiosis of Gislén) has been subjected to very thorough and detailed study, and a series of different associations has been described. The associations of Gislén constitute a much more restricted and specialized unit than the community in the sense of Petersen and that used in the present paper. I do not deny that it may be of great value to have a detailed sociological and ecological description of the fauna of a certain area, similar to that of Gislén in the papers quoted, but when the intention is to get a general view and an opportunity for comparison, it is necessary to try to find more comprehensive units, and in the following short synopsis of the epifaunas I shall not therefore go into detail to such a degree as Gislén.

1. Epifaunistic community of rocks and stones, i. e. the epifauna of which the substratum is rock, stones, shell, etc.

a) *Saxicava arctica* community. This community is primarily characterized by the occurrence of *Saxicava arctica,* attached to stones on the sea-bottom. It is described from the East Greenland fjords (Thorson 1933); it ranges to about the same depths as the *Macoma calcaria* community, and it may be regarded as the epifaunistic community on the bottom corresponding to the *Macoma calcaria* community. It may have a wide distribution in the Arctic.

(b) *Mytilus edulis* community. Characterized chiefly by the occurrence of *Mytilus edulis,* the mussel, and distributed in quite shallow water along the coasts of northern and western Europe, where especially it seems to correspond to the *Macoma baltica* community, and, like this, it also occurs in the Baltic at greater depths than elsewhere. In some localities, for instance, in the Baltic, it is of a certain interest to fishery biology, as the young *Mytilus* may serve as food for plaice and other fishes.

(c) *Modiola modiolus* community. Characterized by the occurrence of the Mytilid *Modiola modiolus,* and by the Ophiurids *Ophiopholis aculata* and *Ophiothrix fragilis,* and several Annelids, crabs and other crustaceans, e. g., species of *Galathea.* This community occurs below the *Mytilus edulis* community and especially in places where the movement and renewal of the water is considerable. It occurs where the current flows strongly in the sounds of the Danish waters, e. g., between Elsinore and Helsingborg (Petersen), and in the sounds between the Faroe Islands and off these islands, on the Faroe Bank and in Faxe Bay at Iceland (Spärck 1929). In these northern

waters it may extend to depths of about 100 m. In Faroese and Icelandic waters it has a fairly wide extension and the amount of living animals may be very great, several kilos per sq. m., the *Modiola modiolus* community is to be regarded as one of the epifaunistic communities of the greatest importance to the food-fishes. The *Galathea* Species and the Annelids of this community especially may serve as food for the cod.

Besides the three communities mentioned above there appear to exist a series of equivalent types in the different waters, but hitherto they have not been investigated in any considerable degree by quantitative methods. As Petersen points out (1915 p. 19) a deeper *Modiola* community characterized by *Modiola phaseolina* may exist, and in the Mediterranean there seem to exist communities characterized by *Modiola barbata, Arca* species, *Lima* and *Ophiotrix fragilis.* Further, there are descriptions of some communities of epifaunas which do not, like the above-mentioned, mainly consist of Mytilids (the "valvosa" of Gislén) but of corals, Ascidians, Hydroids, sponges etc. In deeper waters in the Scandinavian seas we have, for instance, an epifauna of *Lophohelia, Paragorgia,* Brachiopods and *Gorgonocephalus* described by various authors, and on the rocks at the Faroes an *Alcyonidium* epifauna (Spärck 1929), in the Mediterranean an epifauna of *Microcosmus* and other Ascidians (Vatova), and the various associations of "Corallosa" and "Crustosa" described by Gislén from Bohuslän and Japan. In deeper waters in the Arctic we also seem to find different epifaunistic communities of Ascidians, sponges and *Gorgonocephalus* (Spärck 1933). But in spite of a series of such epifaunistic communities having been described from several seas, so little quantitative material is at hand that a more detailed description is restricted to local conditions, and at the present time it seems impossible to obtain a more comprehensive outlook.

2. Besides the epifaunistic communities of rocks and stones there is also the epifauna attached to the vegetation. In this case, too, really quantitative investigations are lacking, and I shall therefore say a few words only on this subject. Here also there seems to be relation between certain communities of the vegetation and the communities of the soft bottoms. Corresponding to the *Macoma calcaria* community and the *Saxicava arctica* community of the Arctic seas, there is a *Margarita groenlandica* community of the vegetation characterized by *M. groenlandica* and by *Modiolaria lævigata* (Thorson 1934). Corresponding to the *Macoma baltica* community of northern Europe there is on the Zostera a *Rissoa* community characterized by *Rissoa* species, *Lacuna divaricata* and other Gastropods. Similar communities on the vegetation will certainly appear in all seas (in Japan cfr. Gislén 1931), but little has hitherto been done from this point of view.

To sum up, we maintain that it has proved possible to describe a few widely distributed communities on the level sea-bottom, and it is further probable that corresponding communities of epifauna exist. The

communities in the above sense are characterized by a combination of a few quantitatively dominant species, but this combination, like the communities, will always be subject to considerable local variations within the range of the community. Petersen simply named the communities after the combination, combining a specific name of one of the characteristic species with a generic name of another. This may seem to be a somewhat impractical method, in the first place because the combination may vary, secondly because naturalists who are not familiar with marine invertebrates may often misunderstand the significance of these names. In the above summary I have therefore named the communities after the animal which seems to be the most characteristic and which is easily recognizable. But it need not be the quantitatively most abundant animal, and it may also be lacking locally, just as in a forest there may be glades and meadows where the dominant trees are absent. When such a characteristic animal is selected, it is extremely important that the quantitative distribution of the fauna over the largest possible areas is known. In 1929 I considered *Thyasira flexuosa* a typical species for the clay bottom about 20—100 m., where it is common in the Kattegat as well as in the Faroese fjords, but it now appears that this species is ubiquitous, occurring in the Mediterranean as well as in the East Greenland fjords, and I now understand that the fauna of the deeper clay bottom at the Faroes and South Iceland represents a poor outpost of the Atlantic and Mediterranean *Amphiura* community.

Considering that the description of the marine fauna by means of Petersen's method provides a comprehensive and general survey, the criticism which may be directed against the exactness of the method becomes less significant. For these general results it is of less importance that the bottom sampler is less successful on hard bottoms, where, as shown by A. C. Johansen by means of Knudsen's bottom sampler, it does not take everything. In this connection the question of the number of samples will also be of less importance, as the differences, when the communities are taken in the wide sense, as above, are so pronounced that a fairly small number of samples will prove sufficient. From a control investigation in 1919 (Spärck and Lieberkind 1921) it further appeared that whether 1800 or 25 samples are taken within the same area the result will be the same for almost all the species as far as their frequency is concerned.

Finally, we shall briefly consider the importance of the quantitative investigations to marine zoogeography[1]) and ecology. It is obvious that the communities described above succeed each other from the south to the north, and they may be arranged in groups according to their geographical distribution. The *Macoma calcaria* community, the *Venus fluctuosa* community, the *Astarte crenata* community and the *Saxicava arctica* community are arctic communities, though the *Macoma calcaria*

[1]) A paper in which the zoogeographical importance will be treated more in detail will appear in "Zoogeographica", Vol. 3.

may, for instance, occur locally south of the Arctic as a survival, or where conditions are similar to those of the Arctic. Some of the species such as *Saxicava arctica* also extend far to the south, but it is only in the Arctic that it is characteristic of a shallow-water community. The *Macoma baltica* community, the *Syndosmya alba* community, the *Modiola modiolus* and the *Tellina tenuis* communities may be considered boreal communities, whereas the *Tapes aureus* and the *Venus verrucosa* communities are lusitanian. Other communities of deeper waters such as the *Venus gallina* and the *Amphiura* communities are of a wider range, and may be considered boreo-lusitanian. Consequently, a relation between the communities and the zoogeographical regions exists, which seems to indicate that among the factors governing the distribution of the communities are also the hydrography and the climate.

Turning to the ecological importance it should be mentioned that the communities are not at all biocoenoses, though they may perhaps, when investigated in more detail, be divided into biocoenoses (cf. the papers of Gislén and Molander). Nevertheless, there is a very clear relation between the communities and some ecological factors, for instance the substratum and the depth, i. e. food conditions. The communities cannot be divided only into geographical groups, but division must also be made into groups according to the bottom. The *Venus fluctuosa* may be considered as the arctic sand-bottom community, the *Venus gallina* community as the boreo-lusitanian sand-bottom community, the *Venus fasciata* community as the boreo-lusitanian shell-gravel community. The *Macoma calcaria* community may be called the arctic soft-bottom coastal community, the *Macoma baltica* the boreal soft-bottom coastal community, the *Tellina tenuis* community the boreal sand-bottom coastal community, the *Amphiura* community the boreo-lusitanian soft-bottom community, etc. It should be possible to name the communities by this method by combining their distribution with the nature of the bottom, instead of applying the name of one of the typical animals, as the present author has done in a Danish book published in 1926 (Nordens Dyreverden). There seems to be no doubt that more detailed quantitative investigations, especially when continued over several years, will be of great importance to the study of the factors governing the distribution of the animals in the sea.

Summary.

1. The quantitative investigations of the bottom fauna by means of Petersen's grab has made it possible to distinguish fairly easily between waters with an abundance of bottom animals, i. e. fish-food, and those with a poor bottom fauna. The differences have turned out to be considerable, and they are related to the depths and to climatological and hydrographical conditions.
2. It is possible to describe a few widely distributed communities characterized by a few dominant animals and to give a general appearance to the fauna of the particular area. These communities

are not biocoenoses, but they are related to the nature of the bottom and to the depth, i. e. to the food-conditions, among others, and to geographical factors, i. e. hydrography and climate.

3. These communities may be arranged in groups according to their geographical distribution, so that it is possible to distinguish between arctic, boreal and lusitanian communities of the different types.
4. These communities can be further divided into types according to the substratum, i. e. soft-bottom communities, sand-bottom communities, epifauna of rocks, vegetation, etc.

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The Annual Organic Production and Nutrient Phosphorus Requirement in the Tropical Western North Atlantic.

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Introduction.

This discussion is dependent upon the following premises:

1. A theoretical calculation of the annual organic production based on a previous estimation of oxygen consumption in the vertical water column within the region of investigation.
2. An estimation of the phosphorus requirements for the above production founded on an investigation of the phosphorus content of oceanic plankton.
3. An inquiry into the sources of phosphorus supply in order to anticipate the approximate correctness of the above results.

Theoretical Estimation of the Annual Production of Organic Matter in the Tropical Western North Atlantic.

The validity of this calculation depends upon two assumptions: first, that an earlier theoretical calculation of oxygen consumption in the whole vertical water column, about 52 cc. per square centimetre of surface per year (Seiwell, 1934), is approximately correct for the region between latitudes 14°N. and 3°N. along the 40th meridian; and second, that this oxygen disappears because of oxidation of the annual crop of organic matter produced in the photo-synthetic layers of the region in question. The validity of the first assumption is discussed in an earlier paper (Seiwell, 1934) while the second assumption appears to be reasonable in the light of general knowledge.

52 cc. of dissolved oxygen disappearing from the water column for

each square centimetre of surface per year is sufficient to oxidize 0.0278 (27.8×10^{-3}) grams of organic carbon, which is assumed to represent the organic production per square centimetre of surface per year (278 grams per square metre) in the region of investigation. This production of carbohydrate may be expressed as 0.0695 grams of glucose per square centimetre (695 grams per square metre) of surface per year[1]), or on the basis of an average carbon content of 49.63 per cent. for oceanic marine organisms studied in this laboratory (Table 2), as being equivalent to about 0.056 grams of dry moisture and salt-free plankton per square centimetre (560 grams per square metre) of surface per year.

Phosphorus Requirements for Organic Production in the Tropical Western North Atlantic.

Carbon and Phosphorus Content of Marine Plankton[2]).

As a means of estimating the phosphorus required for the above theoretical organic production the results of a series of chemical analyses of oceanic plankton are presented. The tow net material for analyses was collected by "Atlantis" in 1932.

Methods. Depths of sampling are approximated from length of wire and visible towing angle at the surface. The tow net material was rinsed twice in distilled water on board before preservation in 95 per cent. ethyl alcohol. To prepare the material for analyses the whole (plankton and preservative) was placed in a large porcelain dish, evaporated to a solid dry mass at a temperature of 50° to 60° C. and then ground sufficiently fine to pass through a screen of 0.5 mm. mesh opening. For analyses small quantities of this rough dried substance were placed in suitable containers, dried at 60° C. for 36 hours and cooled in a desiccator over sulphuric acid before weighing. The analytical results, based on 60° dried moisture-free substance, are given in Table 1. However, for a more rational basis the results in Table 1 have been recalculated in Table 2 on a sea-salt-free basis.

Sea-salt content (S) was estimated by determining the chlorine content of a hot water extract obtained from a small weighed portion of the dried substance and then calculated according to Knudsen's (1901) formula:

$$S = 0.030 + 1.8050\ Cl$$

The results represent sea salts which adhere to the bodies of the

[1]) Pütter (1924) using oxygen observations of "Planet" expedition (Brennecke, 1909) estimated the daily oxygen production by plankton algae at 25 metres depth in the tropical Atlantic to be 1.4 to 2.7 mgm. per litre. Extending these results to one year we calculate from Pütter's data a production of approximately 500 to 900 grams of glucose per cubic metre per year at 25 metres depth. This would indicate production in the whole photosynthetic layer to be several times greater than that estimated from our data.

[2]) Chemical analyses were made in this laboratory by Gladys Eddy Seiwell.

organisms as impurity and that which is contained in their body fluids (see Brandt and Raben, 1920).

Organic carbon was determined by combustion in an open tube according to Liebig (Treadwell and Hall, 1930; duplicate results agreed within 0.1 per cent. of carbon.

Total phosphorus was estimated by the volumetric method for fertilizers of the Association of Official Agricultural Chemists (1925); the ammonium phosphomolybdate precipitate was dissolved in N/2 sodium hydroxide and the excess alkali titrated with standard hydrochloric acid. Triplicate determinations agreed within 0.03 per cent. of P.

Results.

Table 1. Results of analyses calculated on dried (60°C.) moisture-free plankton.

Sample	Depth	Carbon Per cent.	Phosphorus Per cent.	C : P × 10—²	Sea Salt Per cent.
S-II	Surface	29.48	0.46	1 : 1.55	18.0
S-III	100	38.71	1.16	1 : 2.99	22.9
S-IV	500	41.67	1.13	1 : 2.72	7.9
S-V	500	33.28	0.78	1 : 2.34	36.9
S-VII	60 and 150	24.10	0.86	1 : 3.55	44.4
S-IX	Surface	37.38	0.55	1 : 1.47	—[1])
S-X	1500	46.60	1.07	1 : 2.29	14.1
S-XIV	1500	41.43	1.18	1 : 2.85	18.6
S-XV	100	43.37	1.19	1 : 2.75	10.9
S-XVI	1500	35.45	0.91	1 : 2.56	33.3
S-XVII	0 — 15	27.60	0.70	1 : 2.53	43.2

[1]) Material insufficient for estimation of sea salt.

Table 2. Results of analyses in Table 1 recalculated on a sea-salt-free basis.

Sample	Carbon Per cent.	Phosphorus Per cent.	C : P × 10—²
S-II	35.95	0.56	1 : 1.55
S-III	50.2	1.50	1 : 2.99
S-IV	45.2	1.23	1 : 2.72
S-V	52.7	1.24	1 : 2.34
S-VII	43.3	1.54	1 : 3.55
S-X	54.1	1.24	1 : 2.29
S-XIV	50.8	1.45	1 : 2.85
S-XV	48.7	1.34	1 : 2.75
S-XVI	53.1	1.36	1 : 2.56
S-XVII	48.6	1.23	1 : 2.53
Average (exclusive of S-II)	49.63	1.35	1 : 2.73

The tow net material was not examined taxonomically before analyses, but the general nature of the catch can be judged from the following notes.

Sample S-II. "Atlantis" station 1346; 40°45′N., 64°20′W.; Sargassum weed dipped from surface.

Sample S-III. "Atlantis" station 1346; 40°45′N., 64°20′W.; horizontal tow at about 100 metres depth; August 15—16, 1932; time: 23h. 45m. to 01h. 30m.; ¾-metre scrim net. Mixed zooplankton.

Sample S-IV. "Atlantis" station 1346; 40°45′N., 64°20′W.; red prawns from about 500 metres depth taken with 2-metre stramin net.

Sample S-V. "Atlantis" station 1348; 39°36′N., 64°52′W.; horizontal tow at about 500 metres depth with 2-metre stramin net; August 17, 1932; time: 00h. 53m. to 01h. 53m. Mixed zooplankton.

Sample S-VII. "Atlantis" station 1350; 38°33′N., 63°49′W.; horizontal tows from about 60 and 150 metres depth with 2-metre stramin nets; August 18, 1932; time: 00h. 30m. to 02h. 00m. Mixed zooplankton.

Sample S-IX. "Atlantis" station 1352; 36°36′N., 63°37′W.; horizontal tow at surface with No. 20-mesh silk net; August 19, 1932; time: 10:00a.m.; principally Trichodesmium.

Sample S-X. "Atlantis" station 1355; 35°02′N., 62°20′W.; horizontal tow at about 1500 metres with 2-metre stramin net; August 20, 1932; time: 03h. 37m. to 05h. 37m. Mixed zooplankton.

Sample S-XIV. "Atlantis" station 1358; 31°36′N., 64°42′W.; horizontal tow at about 1500 metres with 2-metre stramin net; August 22, 1932; time: 15h. 50m. to 17h 20m. Mixed zooplankton.

Sample S-XV. "Atlantis" station 1362; 33°19′N., 66°30′W.; horizontal tow at about 100 metres depth with 2-metre stramin net; August 28, 1932; time: 21h. 25m. to 23h. 25m. Mixed zooplankton.

Sample S-XVI. "Atlantis" station 1367; 35°17.5′N., 71°27′W.; horizontal tow at about 1500 metres depth with 2-metre stramin net; August 31 — September 1, 1932; time: 22h. 40m. to 00h. 40m. Mixed zooplankton.

Sample S-XVII. "Atlantis" station 1382; 38°13′N., 73°41′W.; horizontal tow between 0 and 15 metres with ¾-metre scrim net; September 5, 1932; time: 02h. 50m. to 03h. 20m. Mixed zooplankton.

Because the towing nets were usually coarse mesh it is probable that no significant amounts of plant material were in any of the tows except S-II (dipped Sargassum weed) and S-IX (principally Trichodesmium). Table 1 indicates that both these plant samples have lower phosphorus content than the others and their carbon phosphorus ratios are nearly equal. For the remainder of the samples both phosphorus (1.23 to 1.54 per cent. P) and carbon content (43.3 to 54.1 per cent.) lay within narrow limits, the averages being 1.35 per cent. P and 49.63 per cent. C (Table 2).

The above results may be compared with analyses of plankton from the coastal waters of northern Europe made by Brandt and Raben (1920); some of which are summarized in Table 3. This material was prepared for analyses by drying to constant weight in vacuo over sulphuric acid and phosphorus pentoxide. The results are calculated on a sea-salt-free basis[1]).

The range of values for phosphorus and carbon found for our

[1]) P_2O_5 results of Brandt and Raben recalculated to P.

Table 3.

	Diatom Plankton (9 samples)	Peridinean Plankton (8 samples)	Copepod Plankton (2 samples)
Phosphorus (P) range (per cent.)	0.40 — 1.59	trace — 1.26	0.375 — 1.14
Phosphorus (P) average (per cent.)	0.96	0.67	0.76
Carbon range (per cent.)	21.69 — 36.25	35.01 — 43.63	48.66 — 51.99
Carbon average (per cent.)	28.77	40.28	50.32

oceanic plankton compare well with the results of Brandt and Raben; the wider range found in their investigation may result from variability of conditions characterizing the environment of plankton inhabiting shallow coastal seas.

Other data on the phosphorus content of marine organisms which illustrate wide variations in relative as well as actual contents of inorganic salts, not only among various varieties of kelp but among the same species as well, are found in Turrentine's compilation of chemical analyses of kelps (1912). The data also suggest that the composition of sea weed may vary with the season. Thus, phosphoric acid content of dried kelp ranges from about 0.08 to 0.93 per cent. P_2O_5 (0.035 to 0.41 per cent. P), the upper limit being close to that found in this investigation for plant samples (Table 1). As suggested by Turrentine the variations of phosphorus content among kelps in his compilation are, perhaps, in part due to occasional use of inadequate methods, both of sampling and analysis, so that the results are not strictly comparable; nevertheless, the variations appear to be great enough to indicate that wide fluctuations may exist among the algae inhabiting coastal seas (likewise suggested by the results of Brandt and Raben, 1920).

The phosphorus content of freshwater plankton appears to be of the same order of magnitude as that of marine organisms; Schuette (1918) obtained a range of 0.91 to 1.57 per cent. P on a series of freshwater plankton samples from Lake Mendota (Wisconsin).

Thus, while the carbon and phosphorus content of marine organisms may be subjected to considerable variability, such variability is, no doubt, to a great extent dependent upon dissimilar environmental conditions[1]) which, from general knowledge, is most pronounced in shallow coastal seas. Hence, it would appear that the average phosphorus content of 1.35 per cent. P and the average carbon content of 49.63 per cent. based on analyses of 9 tow-net samples are

[1]) Evidence that differences in chemical composition of organisms may be correlated with habitat is found in a paper by Clarke and Kamm (1917). See also Clarke and Wheeler (1917).

approximately representative of conditions in the region of investigation; and, for the present, at least, can justly be used for further theoretical speculation.

Before proceeding to calculate the theoretical phosphorus requirement for organic production in the area of investigation an illustration of the differences in relative concentration of phosphorus both in sea water and the plankton is interesting. The greatest recorded average concentration of phosphorus for the 0—50 metre layer of the tropical western North Atlantic was 7 mgm. P per cubic metre[1]), occurring at "Atlantis" station 1174 (8°20′ N., 40°45′ W.; Seiwell and Seiwell, 1934). This is equivalent to a ratio of about 1 part of phosphorus to 1.5×10^8 parts of water, while that for the average phosphorus content of dry plankton is 1.35 per cent. or a ratio of 1 part of phosphorus to 74 parts of dried sea-salt and moisture free material, or 2×10^6 times as much phosphorus in plankton as is in solution in sea water. In other words, in order to produce one gram of dry plankton in the phosphate-richest water of the 0—50 metre layer of the tropical western North Atlantic all of that element which is dissolved at any one time in about 2 cubic metres of water would be required.

Consumption of dissolved Phosphorus.

This calculation is based on the previously estimated annual organic production of 0.056 grams of dry moisture and salt free plankton per square centimetre of surface area (page 21) having an average P content of 1.35 per cent.

The phosphorus (P) requirement is then estimated to be: 0.056 gms. $\times$ 1.35 per cent. $= 75.6 \times 10^{-5}$ gms. sq. cm./year of dissolved phosphorus (7.56 gms. per square metre) for each square centimetre of surface area of the photosynthetic layer per year.

Sources of Supply of dissolved Phosphorus to the Layer of Photosynthesis in the Region of Investigation.

In the region of investigation the supply of dissolved Phosphorus to the photosynthetic layer may be brought about by:

1. Horizontal currents,
2. Regeneration from decaying organic debris within the photosynthetic layer itself,
3. Turbulent movements of the water column bringing up dissolved phosphorus from the rich underlying midstratum.

Supply by horizontal currents. This source is considered to be of secondary importance in the region of investigation because of the low phosphate content of the surface layer[2]). This

[1]) Not corrected for salt error. See Kalle (1934).

[2]) The observations of Hentschel and Wattenberg (1930) and Seiwell and Seiwell (1934) indicate that the surface layer of 50 metres thickness in the tropical western North Atlantic, west of longitude 40°W., usually has an average phosphate (P) content of 2 mg. or less per cubic metre.

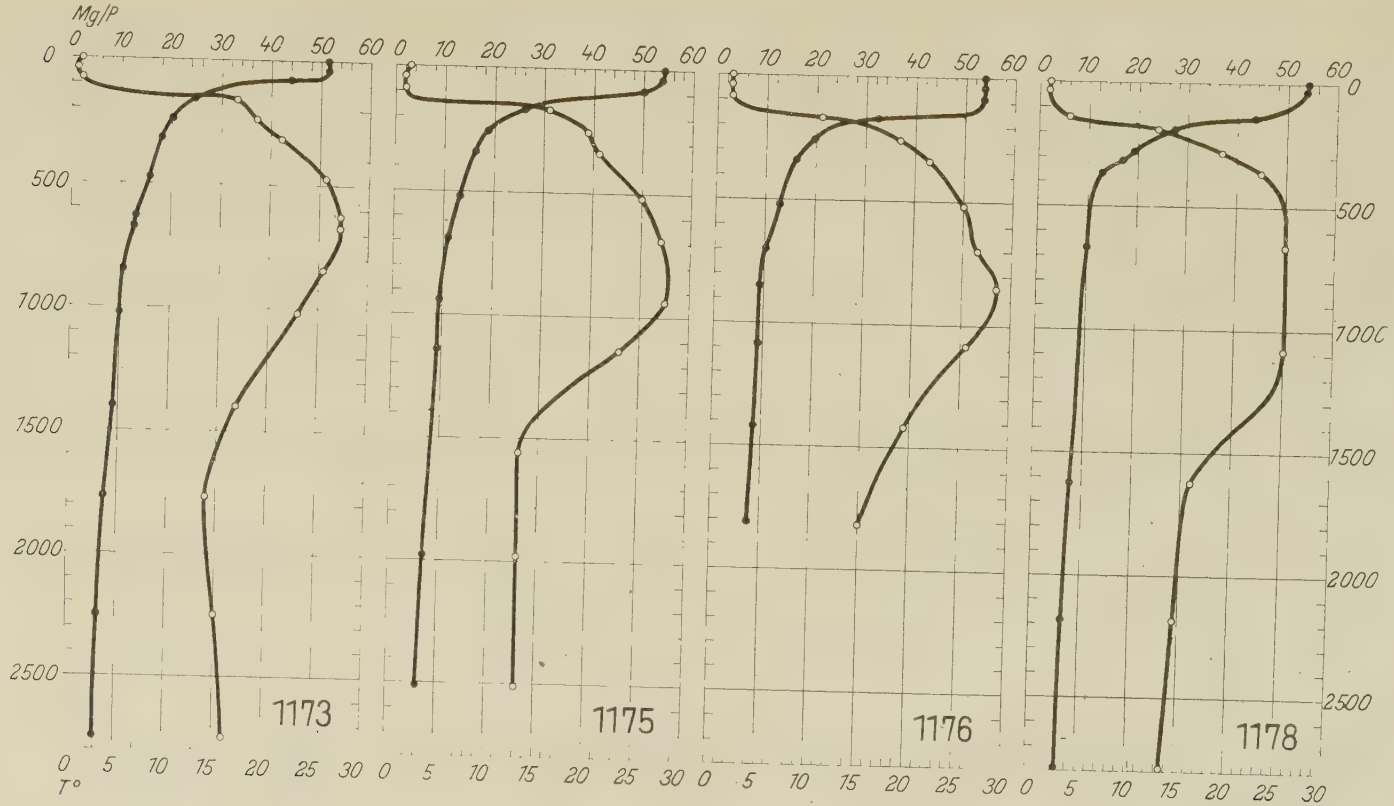

Fig. 1. Vertical distribution of dissolved phosphorus (P) and temperature at "Atlantis" stations 1173 (9°57′N., 40°55′W.); 1175 (6°50′N., 40°25′W.); 1176 (5°16′N., 39°47′W.); 1178 (2°02′N., 41°18′W.). Observations obtained March 16 to 20, 1932; not corrected for salt error.

condition indicates that only a small supply of that element is available for utilization at any one time, although it is conceivable that both the rate of supply and rate of utilization may be rapid.

Supply by regeneration within the photosynthetic layer. That some decay of organic debris and resolution of inorganic phosphorus occurs within the layer of photosynthesis is highly probable. It would appear from the vertical distribution of density in the region (Fig. 1) that when the discontinuity layer lies partly within the depths at which photosynthesis normally occurs (within 50 metres of the surface) sinking of dead organisms is retarded, thus giving sufficient time for resolution of nutrient substances so that they are available for immediate consumption.

Supply by turbulence from the phosphate-rich midstratum. The vertical distribution of dissolved phosphorus in this region (Fig. 1) suggests that a considerable part of the nutrient phosphorus supply to the layer of photosynthesis comes from the phosphate-rich midstratum resulting from a vertical transfer of water particles by eddy movements of the water. This transfer is of small magnitude as it must act through the stable boundary zone separating the phosphate-rich midstratum from the phosphate-poor surface layer[1]) (Fig. 1). And, as the amount of dissolved phosphorus transferred per unit of time will depend both upon its vertical distribution and the magnitude of the eddy movements (coefficient of eddy conductivity), we shall reverse the usual process of reasoning and calculate the upper limit of the eddy coefficient (A) theoretically required at the time of observation to transport annually 75.6×10^{-5} grams of dissolved P for each square centimetre of surface from the phosphate-rich midstratum into the phosphate-poor surface layer. This value of A will then indicate in a general way the relative importance of eddy transfer as a factor in the fertility of the region. Data on the magnitude of eddy coefficients existing in the sea are meager, but from general knowledge we estimate it under present conditions as being somewhere in the vicinity of 2 C. G. S. units[2]).

The coefficient of eddy conductivity, A, may be calculated by the formula:

$$A \frac{dP}{dZ} = N$$

where A is the eddy coefficient; $\frac{dP}{dZ}$ the phosphate gradient over the best developed part of the discontinuity layer; and N the phosphorus required (75.6×10^{-5} grams per square centimetre of surface per year).

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[1]) Eddy conductivity is relatively small in water having great vertical density gradients as in the case under examination. For discussion see Helland-Hansen, 1930.

[2]) See calculated values for eddy conductivity coefficient in water by Schmidt (1925).

The results of the calculation for three positions in the region of investigation ("Atlantis" stations 1172, 1174, 1176) are given in Table 4.

Table 4.

Station	Discontinuity Layer		A
	Depth range	P range	(C. G. S. units)
1172	100 — 180	0 — 30	6.4
1174	30 — 100	5 — 33	6.0
1176	110 — 200	3 — 33	7.3

Thus, the value of A required under the given conditions to transport upward by eddy conductivity all the dissolved phosphorus needed for organic production from the phosphate-rich midstratum into the phosphate-poor surface layer lies between 6 and 8 C. G. S. units. As this value is probably greater than that which represents the normal eddy transfer we may assume that not all of the soluble phosphorus in the photosynthetic layer, but an appreciable part of it, is the result of transfer by eddy movements of the water particles. Thus, since various amounts of dissolved phosphorus may be supplied to the photosynthetic layer from other sources and also as some photosynthesis may occur in the upper part of the phosphate-rich midstratum it would appear that the annual phosphorus (P) requirement of 75.6×10^{-5} grams per square centimetre of surface (7.56 grams per square metre) is within the correct magnitude for the region of investigation.

Comparison of Productiveness of the Tropical Western North Atlantic with other Areas.

If we assume for the present that the magnitude of organic production previously calculated is approximately correct for the region of investigation we may endeavor to compare it with other marine areas. For this, results obtained from studies of the accession or deduction of dissolved substances from the sea water are used here.

Several methods may be used to evaluate organic production, but results of measurements of oxygen production and of phosphate consumption occurring during phytoplanktonic growth appear to be most convenient for this comparison. Both methods have their limitations. Measurements of oxygen production can be had only at times when the phytoplankton is predominant, e. g., during the great spring diatom flowering in boreal coastal waters, so that the use of this method is necessarily restricted to evaluating production over short intervals of time. Also, because some oxygen resulting from photosynthesis is lost to the atmosphere and some is consumed by respiration of plants and animals, the production calculation on this basis will be a minimum one. On the other hand, results of carbohydrate synthesis calculated on the basis of oxygen production are directly comparable with those obtained on the basis of oxygen consumption.

The estimation of dissolved phosphorus consumed from the water column by phytoplanktonic growth can be conveniently made over long periods, but it is difficult to obtain accurate results because continuous regeneration of phosphate of unknown magnitude occurs during the vegetative season, and because horizontal movements of water may make it impractical to observe the same water mass throughout the entire period of investigation. This method also has the disadvantage that it is not possible with any degree of certainty to reduce phosphate consumption to terms of carbohydrate production because phosphorus requirements of marine organisms are not generally known. Thus, an average phosphorus content of 1.35 per cent., tentatively taken as representative for tropical oceanic organisms cannot be said to represent that for organisms living in the coastal seas of northern Europe. To illustrate this point we find that Atkins (1923) estimated the phosphorus (P_2O_5) content of Nitzschia to be 0.15 per cent. of their wet weight and the hexose sugar content at 15 per cent. Thus, the ratio of carbon to phosphorus (P) on this basis works out to be 1 to 1.09×10^{-2}. On the other hand, Brandt and Raben's (1920) results of 30 analyses of marine organisms (principally plant plankton) showed an average ratio of 1 part of carbon to 1.87×10^{-2} parts of phosphorus (P); while the results of analyses of net plankton (principally animal) made in this laboratory show an average ratio of 1 part of carbon to 2.73×10^{-2} parts of phosphorus (P). Hence, until better data are available, any comparisons of organic production on the basis of dissolved phosphorus extracted from the water must necessarily be crude.

Comparison with Daily Production in the Coastal Waters of Northern Europe during Diatom Flowering.

In the coastal waters off Bergen (Norway) during 3 weeks in March 1922, Gran (1927) observed an oxygen increase of about 1 cc. per litre in the surface layers coinciding with diatom development. This is equivalent to a theoretical production of 1.4 grams of glucose per cubic metre in the surface layers, and as Gran estimates the production to be representative to a depth of 10 metres, the approximate production during the 3-week period is placed at 14 grams of glucose per square metre of surface over an area extending from the coast out to a distance of approximately 40 miles; or a daily production of about 0.7 grams of glucose per square metre of surface. Another calculation by Gran (1929) for production on the bank of Romsdalsfjord (Norway) in March 1927 gave estimated values ranging from about 0.3 to 1.5 grams of glucose per square metre of surface per day.

Comparing the above values with those for tropical waters of the western North Atlantic it may be assumed that in the latter locality production from day to day is approximately uniform. Hence, an annual production of 695 grams of glucose per square metre of surface would be equivalent to a daily production of 1.9 grams which is slightly higher than the maximum value obtained by Gran. However, as

culture methods give results almost 4 times as high as those obtained by direct observation (Gran, 1927) of oxygen increase in the water it is possible that daily production during the diatom maxima of northern Europe may be about 3 to 4 times as great as that of the tropical western North Atlantic[1]).

Comparison with Annual Production in Coastal Seas of Northern Europe.

In the Barents Sea during the vegetative season of 1930, Kreps and Verjbinskaya (1932) estimated that dissolved phosphorus consumed in the water column to 200 metres depth, ranged from 5.620 to 8.400 grams P_2O_5 per square metre of surface (2.99 to 3.66 grams of P)[2]). This is equivalent to an annual phosphorus consumption of about one-half to one-third of that calculated for the tropical waters of the western North Atlantic. However, in view of the previous discussion of phosphorus requirements, the organic production of the two regions is probably not in the same proportion as the apparent phosphorus consumption. In this connection Kreps and Verjbinskaya (1932) calculated production in the Barents Sea in terms of "wet weight" phytoplankton, using Atkins's (1923) estimate that the phosphorus content of the "wet weight" phytoplankton is about 0.15 per cent., and arrived at values ranging from 428 to 840 grams of glucose per square metre of surface. On this basis the total annual organic production would be 0.6 to 1.2 times that calculated for the tropical western North Atlantic.

In the English Channel, Atkins (1923) and later Cooper (1933) calculated the annual plankton crop off Plymouth (England); Cooper, from an average phosphate consumption of about 20 to 26 milligrams P_2O_5 per cubic metre, estimated an annual phytoplankton production of about 1200 metric tons[3]) (wet weight) per square kilometre of surface, or 180 grams of glucose per square metre of surface. This would be only about one-fourth of the calculated annual production in the tropical western North Atlantic. As the estimate is based on an average depth of 72 metres it represents a phosphorus consumption of about 7.5×10^{-1} grams of P per square metre of surface per year, or only about one-tenth of the dissolved phosphorus consumption calculated for the tropical western North Atlantic.

Hence, on the basis of evidence at hand it appears that the annual phosphorus consumption in the coastal waters of high latitudes of the North Atlantic is only about one-tenth to one-half as much as that estimated for the tropical western North Atlantic; but it does not follow that the annual productions of organic matter are in the same

[1]) Pütter (1924) calculated an average daily production of 34 grams of glucose per square metre of surface for Kiel Harbor during summer.

[2]) Tentatively corrected for regeneration during vegetative period, but uncorrected for salt error.

[3]) On the basis of salt error correction for phosphate values Cooper (1934) later corrected this value to 1400 metric tons.

proportion. Such comparisons must, for the present, remain indefinite. Using Atkins's (1923) ratio of phosphorus content of brown algae the annual production in two northern European waters (Barents Sea and English Channel) would be about 0.25 to 1.2 times that of the tropical western North Atlantic; whereas the carbon phosphorus ratio of Brandt and Raben (1920) places production at 14 per cent. for the English Channel and 44 to 70 per cent. for the Barents Sea. However, even if these values are approximately correct, the amount of organic matter produced during the short growing season of high latitudes would be at least equal to and probably several times greater than that of the tropical western North Atlantic during an equal period of time.

Abstract.

In the tropical western North Atlantic ocean the annual production of carbohydrate is calculated to be 695 grams of glucose per square metre of surface area. This calculation is based on an earlier estimation that the annual oxygen consumption in the water column of approximately 52 cc. per square centimetre of surface area (52×10^4 cc per square metre) represents the amount required to oxidize organic materials produced in the photosynthetic layers under a similar unit of surface per annum. The annual dissolved Phosphorus (P) requirement for photosynthesis is estimated to be 75.6×10^{-5} grams per square centimetre of surface (7.56 grams per square metre) based on a ratio of 1 part of carbon to 2.73×10^{-2} parts of phosphorus (P) for oceanic plankton. An investigation of the agencies supplying phosphorus to the photosynthetic layer appears to indicate that a relatively large part of the soluble phosphorus comes from the phosphate rich midstratum through eddy movements of the water. While it is doubtful if all dissolved phosphorus is supplied in this way, there are other sources of supply so that 75.6×10^{-5} grams of P per square centimetre of surface appears to be within the approximately correct magnitude of that utilized during phytoplanktonic growth in one year.

A comparison of phosphorus consumption in the tropical western North Atlantic with that in the English Channel and Barents Sea indicates that in these latter regions only one-tenth to one-half as much phosphorus is consumed annually; while attempts to compare the total organic production indicate it to be 0.25 to 1.2 times as much. At best, however, because of a number of indeterminate variables these comparisons are indefinite.

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The Determination of Iron in Sea Water.

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IN a recent publication, the authors (3) outlined a method for the determination of iron in sea water, giving the results of a number of analyses. As the method had several undesirable features, further study was accorded it with the idea of increasing its accuracy and sensitivity. This has been accomplished and the modified method is described below.

Reagents.

All the reagents should be tested to insure their freedom from iron.
Potassium Permanganate. Dissolve 6.30 grams of the salt in 1 litre of distilled water.
Bromine Water. A few drops of liquid bromine are introduced into distilled water to obtain a saturated solution. It has been found that if this reagent is stored for some time, it may leach out some of the iron contained in the glass bottle. Thus fresh solutions should be utilized.
Potassium Thiocyanate. Dissolve 480 grams of the salt in distilled water to make a stock solution of four litres.
Isoamyl Alcohol. The liquid should be water-clear. Boiling point 128—132°.
Sulfuric Acid. It is possible to secure iron-free sulfuric acid on the market but the ordinary reagent grade may contain sufficient iron to make distillation of the acid necessary.
Sodium Sulfate. The ordinary pure chemical contains enough iron to decidedly interfere with the determination. It may be rendered practically free of iron by the following procedure: Enough of the salt is dissolved to make three litres of a solution saturated at 20°C.

The solution is acidified with 1 ml. of concentrated sulfuric acid, heated to boiling, and bromine water added to give a distinct yellow tinge. The bromine is boiled off and 1 ml. of a saturated solution of sodium hydroxide is added in excess of the amount required for neutralization. The solution is stirred, allowed to cool to 20°, seeded with a crystal of sodium sulfate to make sure that it is just saturated, and filtered through a fine filter. The filtrate is slightly acidified with sulfuric acid and is then ready for use.

Standard Iron Solution. To prepare stock solutions for use in making up iron standards 403 mg. of ferrous ammonium sulfate is dissolved in 50 ml. of water, 20 ml. of 6N sulfuric acid are added, and permanganate reagent introduced into the hot solution until the color persists for five minutes. A few millilitres of bromine water are added to decolorize the solution, which, after boiling to expel excess bromine, is transferred to a volumetric flask, and made up to a volume of one litre. One ml. of this solution, if diluted to 100 ml., by adding the proper amounts of sodium sulfate solution and distilled water, will give a solution analogous to that obtained from a sample of sea water, containing 0.01000 mg. atoms of iron per kilo. Since the iron content of sea water is usually far below this value the solution is twice diluted to form the two more dilute stock solutions, which will give standards containing 0.00100 and 0.00010 mg. atoms of iron per kilo. when similarly treated. In the preparation of each stock solution, 1 ml. of 36N H_2SO_4 should be added in order to eliminate the hydrolysis of ferric sulfate. Two sets of standard solutions should always be prepared in order to check one against the other and checks with a fresh standard should be made every few months.

Procedure.

In determining iron in sea water, one of the chief sources of possible contamination is particles of iron rust from the cable used in the collection of samples. All the waters studied by the authors, with the exception of the seasonal samples, were collected from the M.S. "Catalyst" which is equipped with a stainless steel cable.

A 100 ml. sample of sea water is introduced into a 500 ml. pyrex Erlenmeyer flask, covered with a watch glass, 6 ml. of 36N sulfuric acid added and evaporated to sulfuric anhydride fumes.

The hot plate on which the evaporation is performed should be made preferably of material other than iron. If an iron plate must be used, it should be thoroughly cleaned and covered with aluminium paint or other material that will withstand changes of temperature without cracking and prevent contamination of the samples with dust of iron rust. It has been found that anhydrous sodium sulfate forms a very satisfactory coating for an iron plate and prevents possible contamination. To apply this coating, the plate should be thoroughly cleaned, heated to its maximum temperature, and then daubed with a cloth saturated with a solution of sodium sulfate. The hard, white

coating adheres tenaciously to the surface and is very stable provided it is not moistened when cold.

After evaporation is complete, the sample is strongly fumed over a Meeker burner to insure complete removal of volatile substances, particularly fluorides (4), which interfere with the thiocyanate reaction. The flask is placed on an asbestos board, and allowed to cool to about 100° C., when 80 ml. of distilled water are poured in and the contents of the flask stirred and boiled to insure solution of the salts. If the flask is permitted to cool much below 100° before the addition of the water, the solution of the salts can be accomplished only with marked difficulty. Potassium permanganate solution is added drop by drop to the hot solution, until the characteristic color of the permanganate ions persists for at least five minutes; two drops have been found to be sufficient in most cases. The permanganate insures the destruction of any organic matter, the presence of which would retard the thiocyanate reaction. The excess permanganate is decolorized by the addition of a few millilitres of bromine water. After boiling off the excess bromine, the solution, which should have a volume of about 45 ml., is allowed to come to room temperature.

The cool solution is transferred from the Erlenmeyer flask to a 125 ml. separatory funnel and made up to about 85 ml. with distilled water. It is then mixed with 10 ml. of potassium thiocyanate solution, and the resulting colored material is extracted by shaking out with 10 ml. of isoamyl alcohol. The water layer is drained off, and after jarring the adhering water down into the tip of the funnel, and removing it, the clear alcoholic layer is transferred to a labelled, dry test-tube. A very small quantity of water in the test-tube will interfere with the colorimeter comparison and tend to make the solution cloudy. After treating about thirty samples in this manner, they are roughly segregated, by inspection, into three groups to be compared with the 0.00025, 0.00100, and 0.00200 mg. atoms per kilo. standards respectively. They are compared in a Klett colorimeter.

Preparation of Standards.

From one to three standards, containing 0.00025, 0.00100 or 0.00200 mg. atoms of iron per kilo. are made up by adding 2.5 ml. of the most dilute stock solution and 1 and 2 ml. of the least dilute stock solution, respectively, to measured volumes of the sodium sulfate solution contained in 500 ml. Erlenmeyer flasks. The necessary volume of sodium sulfate is determined from

$$\text{Volume of } Na_2SO_4 \text{ Solution} = 1.3 \times 0/00 \text{ Cl}$$

where 0/00 Cl is expressed as whole numbers. A variation of one unit made no appreciable difference. The standard iron solutions are measured with a microburet, but the use of a graduate suffices for the sodium sulfate solution. After the addition of 5 ml. of 36 N H_2SO_4, the solutions are brought to room temperature, treated with potassium thiocyanate and the colored substance extracted with isoamyl alcohol

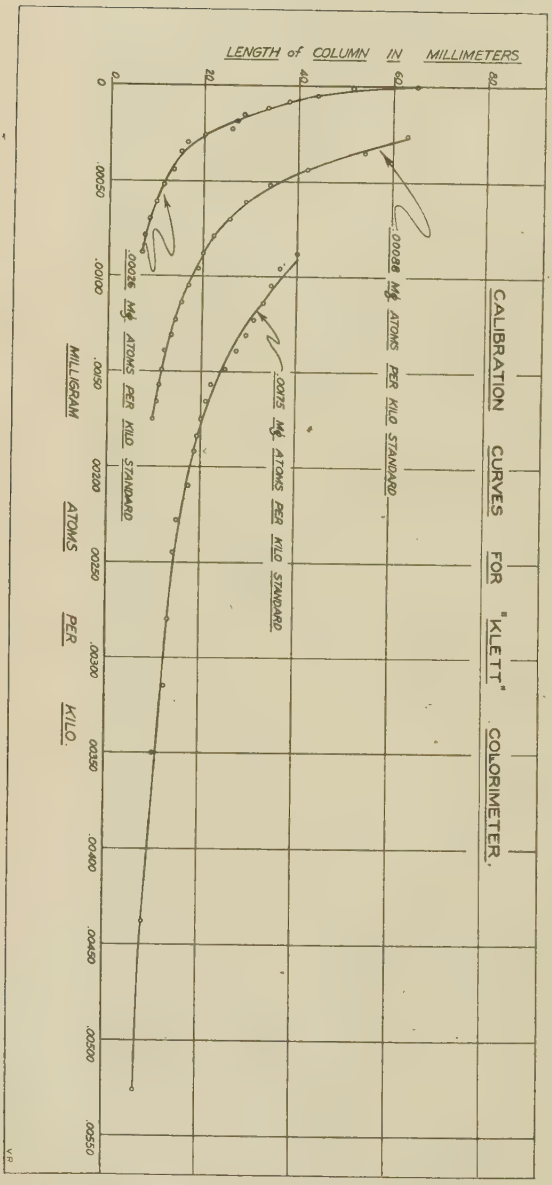

Figure 1. Calibration curves for "Klett" colorimeter, obtained by plotting the data given in Table 1.

Table 1.

Calibration of "Klett" Colorimeter.

With Standard 0.00026 Fe		With Standard 0.00088 Fe	
Milligram Atoms Fe 10^5	Height of Plunger mm.	Milligram Atoms Fe 10^5	Height of Plunger mm.
00	65.0	26	63.0
2	51.5	35	54.0
5	44.0	44	42.0
9	38.0	52	34.0
12	33.5	61	29.0
16	28.5	70	25.5
19	27.0	79	22.2
23	25.8	88	20.0
26	20.0	96	19.0
30	16.7	105	17.0
35	15.2	114	15.7
44	13.8	123	14.3
52	11.4	131	13.3
61	10.0	139	12.0
71	8.6	149	11.4
79	7.6	157	11.0
88	7.0	166	10 5
		175	9.7

With Standard 0.00175 Fe

Milligram Atoms Fe 10^5	Height of Plunger mm.
88	40.0
96	36.5
105	34.6
114	33.0
123	31.0
131	29.5
139	27.5
149	25.0
157	22.0
166	21.0
175	20.0
184	19.2
192	18.7
210	17.5
228	15.0
245	14.2
280	13.3
315	12.5
350	10.2
438	8.3
526	6.7

after about half of the sea water samples have been so treated. In this manner the small error which might be produced by changes on standing different lengths of time are reduced.

Calculation of Data.

Beer's law is not applicable, except over short ranges of concentration. It has therefore been necessary to construct a graph for each standard used. A 20-mm. column of standard in one cup of the colorimeter was used in doing this, and all samples are computed on that basis. The data for the graphs were obtained by making up known solutions containing 0.00000 to 0.00088; 0.00026 to 0.00175; and 0.00088 to 0.00526 mg. atoms of iron per kilo. and running these with 0.00026, 0.00088, and 0.00175 mg. atoms per kilo. standards, respectively. Examples of the data thus obtained and the corresponding graphs are given in Table I and Figure 1. The iron content of a sample can be read directly from the appropriate graph. The graphs are not to be recommended for use as shown, on account of the individual differences of various observers. Each observer should therefore construct his own graphs.

Discussion and Notes.

K e n n e d y (1) has used isoamyl alcohol, under entirely different conditions, for the extraction of the ferrithiocyanate ions. Under the conditions prevailing in the present method for the determination of iron in sea water, a minimum of 0.00002 milligram atoms of Fe (approximately 0.001 mg. of iron per litre) may be detected by extracting with isoamyl alcohol. K e n n e d y's statements that the color is stable toward light and unstable toward heat have been confirmed, but the authors find that by no means does the color conform to Beer's Law under the conditions prevailing in sea water.

L e a v e l l and E l l i s (2) have recently published a paper showing the mercaptoacetic acid method to be more delicate than the thiocyanate-isoamyl alcohol method when used for the determination of iron in milk and blood. We have not attempted to use the mercaptoacetic acid reagent in sea water, but since we are able to detect a minimum of 0.001 mg. of iron per litre by the other method, using only 100 ml. samples, the actual quantity of iron detectable is 0.0001 mg., or considerably less than the 0.0025 mg. reported by L e a v e l l and E l l i s.

The alcoholic extract has a comparatively stable color which is many times as intense as that of the water solution before extraction. One-tenth as much iron may be detected by this process as can be detected in the water solution, using 100 ml. Nessler tubes. It should be noted, however, that if the alcohol solution is cooled a few degrees, some of the dissolved water separates, rendering the solution cloudy, and centrifuging is necessary. The temperature of the laboratory should therefore be maintained approximately constant during the

extraction to eliminate this extra step. On account of the instability of the complex ion $[Fe(CNS)_6]^{=}$ in water solution, the temperature before extraction with alcohol has a decided effect upon the color obtained. The color is much more stable toward heat in the alcohol solution than in water solution. For these reasons it is recommended that all samples be allowed to come to complete temperature equilibrium before the addition of thiocyanate reagent.

The color changes somewhat, but after the first half-hour total light transmitted, as observed with the Klett colorimeter at about 26° C., remains approximately constant. Table II was obtained by comparing 0.00026, 0.00088 and 0.00175 mg. atoms per kilo. standards with 20 mm. columns of freshly prepared 0.00088 mg. atom per kilo. standards by means of the Klett colorimeter and thus illustrates the stability of the isoamyl alcoholic solution.

Table 2.

Time	mg./l. 0.00026	mg./l. 0.00088	mg./l. 0.00175
11:30 — (Standards were prepared)			
	m. m.	m. m.	m. m.
12:05	56	20	10
12:40	55	20	10.5
1:10	50	20	10.5
2:25	49	20	10.5
3:40	50	19.5	10.5
4:20	50	19	10.5

About 75 per cent. of the isoamyl alcohol used may be recovered by destillation in the presence of sodium hydroxide. The fraction collected between 128° and 132° is used. Redistillation of the lower boiling fraction yields a considerable quantity of alcohol within the desired boiling point range.

Conclusions.

1. A method has been described for the determination of iron in sea water capable of detecting as low as 0.00002 milligram atoms (about 0.001 mg.) of iron per kilo.

2. Fluorides and organic matter interfere with the determination and must be removed.

3. Errors that might be produced by the presence of sulfate ions are compensated by the preparation of standards containing equivalent quantities of these ions.

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The Occurrence of Iron in the Waters of the North-East Pacific Ocean.

By

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ALTHOUGH widely varying reports (1) (2) (4) (7) (8) on the quantity of iron present in sea water had appeared in the literature the first attempt to observe possible changes with depth and with the seasons were reported in 1932 by the authors (5). Most of the data presented at that time were obtained from samples of sea water collected in the Puget Sound area and the Strait of Juan de Fuca; and no special precautions to distinguish between filtered and unfiltered samples were taken. It was shown that the iron content increased with depth, that its concentration was materially affected in passages where there was marked turbulence of the waters and that the phytoplankton evidently was one of the factors in causing the removal of the iron from the water. The soluble iron does not occur in the form of simple ferric or ferrous ions, but as complex compounds both of an organic and inorganic nature.

The presence of fluorides (6) and of organic matter in the water prevented the determination of iron by any of the ordinary methods and a means for removing these interfering substances was described. However, the method then proposed had several objectionable features which have been materially altered, and its accuracy and sensitivity decidedly improved by the authors as described in the preceding article.

Seasonal Variations in the Iron Content of Sea Water.

Beginning in 1931 and extending over a period of two years, with the exception of three months in 1932, surface samples were collected in San Juan Channel from the Observation Platform of the field

Table I.

Seasonal variations in the concentration of iron in sea water.
Friday Harbor, Washington.
Results reported as Milligram Atoms per Kilogram.

	1931—1932		1932—1933		Monthly Averages	
	Total Iron 10^5	Soluble Iron 10^5	Total Iron 10^5	Soluble Iron 10^5	Total Iron 10^5	Soluble Iron 10^5
October	123	96	102	37		
	123	80	128	86	119	75
November	158	80	152	105		
	150	105	180	82	159	93
December	210	105	150	30		
	158	105	185	80	175	82
January	140	53	177	126		
	100	30	184	107	150	79
February	145	53	168	47		
	145	75	150	35	152	53
March	135	100	107	70		
	21	21	58	10	93	57
April	23	0	160	28		
	37	—	86	31	75	30
May	35	—	65	31		
	18	—	58	26	61	28
June	0	—	72	25		
	—	—	56	40	60	33
July	—	—	30	10		
	—	—	65	45	47	28
August	—	—	65	28		
	—	—	—	—	65	28
September	—	—	58	40		
	—	—	120	45	89	44

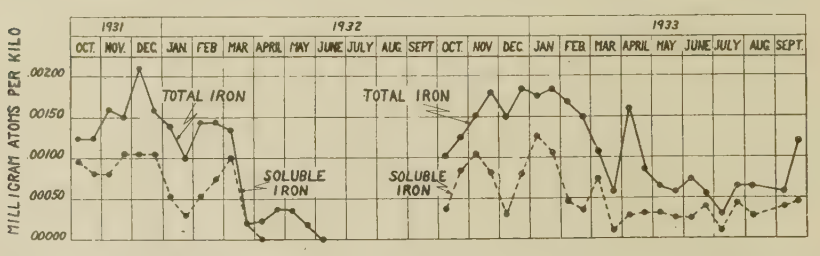

Figure I. Semimonthly averages of iron content of sea water at Friday Harbor, Washington, plotted from the first four columns of Table I.

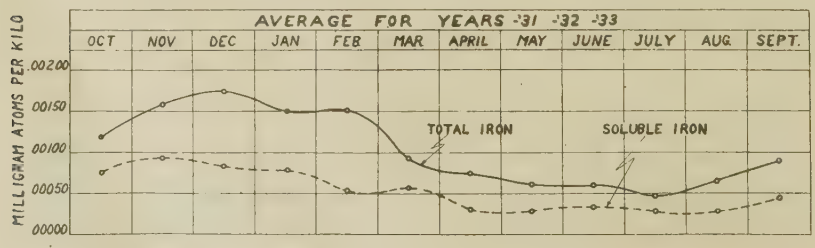

Figure II. Monthly averages of iron content of all the samples analyzed at Friday Harbor, Washington, plotted from the last two columns of Table I.

laboratories at Friday Harbor, Washington. Samples were secured about seven times monthly near the peak of the flood tide, and on each occasion two 100 ml. samples of unfiltered and two of filtered water were taken, acidified with 6 ml. of iron-free 36 N sulfuric acid and stored in seasoned 500 ml. Erlenmeyer flasks, carefully covered, until analyzed.

The unfiltered samples were analyzed for total iron and the filtered samples for soluble iron. Whatman # 42 filter paper was used with gravity filtration and appeared to give the most consistent results.

The insoluble iron, as represented by the difference between the total and the soluble iron, may be attributed to the presence of the element contained in very finely divided inorganic material deposited by the rivers or washed into the sea from the sea-shore or carried up from the irregular bottoms by tidal or other currents. It also represents the iron contained in microscopic organisms, particularly phytoplankton.

The data obtained on analysis are given in the first four columns of Table I and illustrated in Figure I. Each number represents the average of three or four different checked analyses, and these averages are shown for the first and last parts of each month. The last two columns in Table I, which are shown in Figure II, consist of monthly averages of all samples for the two years and show the general trends of seasonal variation. Considerable fluctuation in both soluble and total iron content were observed from sample to sample. Thus the curves most characteristic of seasonal changes are obtained by plotting averages of considerable numbers of individual determinations.

The fluctuations may be attributed to a number of causes, such as the rate of discharge of the larger rivers affecting the region over a considerable area, the local run-off in the immediate region due to rains, the quantities of suspended material carried into the waters by drainage, the nature and height of waves beating upon the shores of the region, the strength of the tidal currents which would create a turbulence and thus carry into the supernatant waters fine materials previously deposited on the bottom, and also the variation in tidal conditions during a given month.

The data show a large degree of parallelism between the total and soluble iron content. Both curves rise to a maximum during the winter months and fall to a minimum during the summer. The most rapid decrease in iron content occurs during the latter part of March and the principal increase occurs during September and October. The average spring-summer (60 checked samples) and fall-winter (75 checked samples) values are given in Table II where spring-summer is considered as extending from March 15th to September 15th.

Table II.	Spring – Summer mg. at./kilo	Fall – Winter mg. at./kilo
Total Iron	0.00053	0.00147
Soluble Iron	0.00026	0.00075

Thus approximately half of the iron is seen to be in the soluble form and there is about one-third as much iron present in the summer as in the winter.

During the fall-winter periods there is a considerable rainfall throughout the Puget Sound region with practically no snow, while in the spring-summer periods the rainfall is very much less and is practically nil during the months of July and August. However, several of the great rivers of this region are fed by the melting of the heavy snow falls in the mountains *back* of the Cascade and Coastal ranges and generally flood conditions will be encountered for short periods during the months of May, June, and even July. The rivers that rise *in* the Cascade and Coastal ranges, while in flood stages generally during the late fall and winter months, carry large quantities of suspended material to the sea but during the spring and summer the discharge is materially reduced, particularly in the summer months.

The semimonthly values tend to show an inverse relationship between the insoluble iron, as represented by the difference between the unfiltered and filtered samples, and the soluble iron. The soluble iron concentration reaches a low value in April and remains practically constant, until the autumn rise, which begins about the first of September. The total iron, on the other hand decreases steadily to a minimum in July and then begins to increase.

Distribution of Iron in Straits and in Estuaries near the Mouths of Rivers.

Samples were collected a few miles from the mouth of the Fraser River in southern British Columbia, (Sta. 2715.1 and 2715.2), thirty-five miles from the mouth of the Skeena River in northern British Columbia (Sta. 4515.1) and thirty miles from the Stikine River in south-eastern Alaska, (Sta. 3815.1). The data are shown in Table III and illustrated in Figure III. Comparison of these data with those of Table I demonstrate the effect of rivers due to the discharge of suspended material relatively high in iron.

The effect of the summer stratification adjacent to the mouth of the Fraser River, as described by Hutchinson, Lucas and McPhail, (3) is demonstrated for iron in Table III as shown by the high total iron content of surface waters of Stations 2715.1 and 2715.2. There is less noticeable stratification in the case of the more northern rivers, due to the fact that samples were collected at greater distances from their mouths, and the vertical mixing, which occurs in the fall and winter, had already begun.

In all cases the iron contributed by the rivers is shown to be largely in the insoluble form, as the soluble iron is practically constant at all depths near the mouths of rivers. The iron-chlorinity ratios for the soluble iron demonstrate that either there is a small amount of soluble iron discharged by the river, or some of the insoluble iron has been dissolved by the dilute sea water, as the ratio is considerably higher

Table III.

The iron content of samples collected in straits and estuaries near the mouths of rivers.

Depth in meters	Station 2715.1 Total 10^5	Station 2715.1 Soluble 10^5	Station 2715.2 Total 10^5	Station 2715.2 Soluble 10^5	Station 4515.1 Total 10^5	Station 4515.1 Soluble 10^5	Station 3815.1 Total 10^5	Station 3815.1 Soluble 10^5
S	2230	118	920	102	260	71	192	31
10	116		960	137	192	86	35	28
25	128	100	119	93	98	70	180	37
50	700	89	101	96	96	86	210	38
100			117	121	100	52	158	37
150							368	23
275			9470	137				

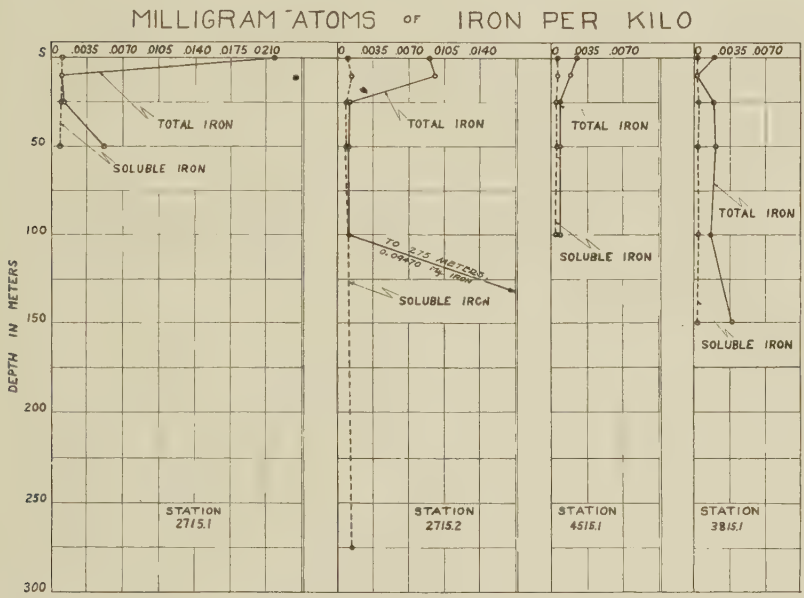

Figure III. Distribution of iron near the mouths of rivers, plotted from the data in Table III.

for the surface waters. The very high values for total iron obtained in the 275 m. (bottom) sample of station 2715.2 was due to the presence of much suspended material from the bottom.

The concentrations of soluble iron in Stations 2715.1 and 2715.2 are several times as large as the values obtained for the summer months at Friday Harbor 35 miles from the mouth of the Fraser River. The concentration thirty miles from the mouth of the Stikine River in south-eastern Alaska, Station 3815.1, is approximately equal to the summer values obtained at Friday Harbor, while that thirty-five miles

from the mouth of the Skeena River in northern British Columbia, Station 4515.1, is about twice as large. The larger quantities of soluble iron at this station may be attributed to the fact that the samples were collected about the middle of September, after the apparent seasonal increase had begun.

Much of the insoluble iron exists in the suspended material discharged by the rivers of the region studied. A large portion of this material is deposited immediately at the mouths of the rivers and it is only the more finely suspended particles, almost colloidal in nature, that are carried seaward in layers of brackish waters floating on the colder and denser sea waters. The brackish layers mix with the sea water due to tidal currents, wind action, irregular bottoms, etc. With increase in the concentration of electrolytes in the surface waters, the particles coagulate and tend to settle. Thus the particles are distributed throughout the entire mass of water. The settling is facilitated upon reaching large basinlike areas, or the coastal planes, where the force of currents may be considerably diminished and at times when the tidal currents, especially in straits and channels, slacken. Much of the sedimentary material on the bottom may be forced into the supernatant waters as currents approach maximum velocities.

The solubility of the particles is greater in sea water than in the fresh waters, and the iron is gradually leached out, that occurring in the ferrous state being oxidized by the dissolved oxygen. The amount of iron entering solution is a function, not only of the size of the particle and the nature of the material, but also of the quantity of

Table IV.

The iron content of samples from the northeast Pacific collected from 25 to 100 miles off the continental shelf.

Results reported as Milligram Atoms of Iron per Kilo.

Depth in meters	Sta. 4922—12929 Total Iron 10^5	Sta. 4922—12929 Soluble Iron 10^5	Sta. 4740—12623 Total Iron 10^5	Sta. 4740—12623 Soluble Iron 10^5
S	93	21	30	4
25	26	26	—	—
50	24	18	32	7
100	42	21	25	5
200	33	21	26	7
300	56	17	26	9
400	30	17	21	9
500	26	16	21	10
600	30	14	32	7
700	35	14	35	18
800	61	14	37	7
900	70	12	34	12
1000	85	16	58	15
1100	61	16	26	18
1200	55	0	26	16
1500	70	23	96	20
2000	53	22		

iron and the concentration of substances capable of forming complex anions with the ferrous or ferric iron. Due to the basic nature of the sea water and the extreme insolubility of ferric hydroxide, little iron would exist in solution if it were not for the fact that the organic matter and the fluoride ions tend to form soluble, stable complexes.

Distribution of Iron in the Ocean off the Continental Shelf.

Iron was determined on filtered and unfiltered samples collected between July 22—24, 1933, in the north-east Pacific off the west coast of Vancouver Island and the State of Washington, from 25 to 100 miles off the continental shelf. The data are shown in Table IV and illustrated in Figure IV. Station numbers indicate latitude and longitude.

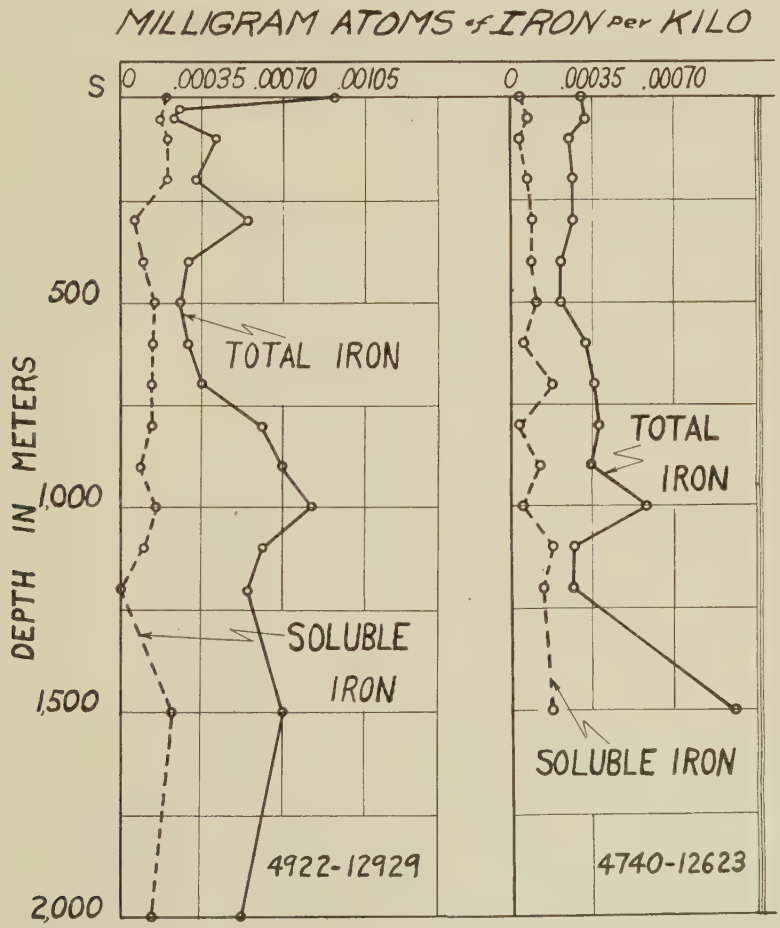

Figure IV. Distribution of iron in the ocean off the continental shelf, plotted from the data in Table IV.

Table V.

The iron content of samples from the Gulf of Alaska collected over the continental shelf, a few miles from Cape Spencer.

Depth in meters	Sta. 5803—13650 Total Iron 10^5	Depth in meters	Sta. 5749—13718 Total Iron 10^5	Soluble Iron 10^5
S	28	S	93	28
10	74	10	91	21
25	26	25	95	
50	79	50	204	21
100	25	100	84	28
200	26	165	250	52
300	70			

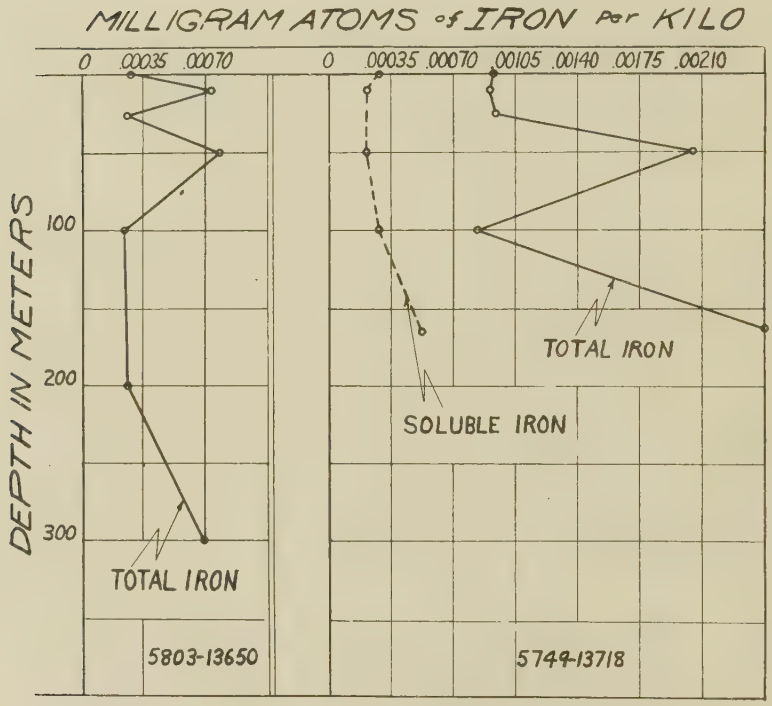

Figure V. Distribution of iron over the continental shelf near Cape Spencer, Alaska, plotted from the data in Table V.

Both the soluble and total iron content of the waters collected beyond the continental shelf are considerably below the values obtained at Friday Harbor, or in any of the straits or estuaries examined. The concentration of soluble iron increases slightly with depth. There are maximum values in total iron at 1000 metres at Stations 4922—12929 and 4740—12623. The influence of suspended material in the waters over the sea floor is shown for Station 4740—12623, where the deepest sample was taken a few meters from the bottom.

In a recent paper by Thompson, Thomas and Barnes on the distribution of dissolved oxygen in the north-east Pacific and Bering Sea it was shown that a region of minimum oxygen values existed at depths between 800 and 1100 metres. Oxygen occurred in exceedingly small amounts at these depths and it was postulated that this water undoubtedly had had contact with the sea bottom for a considerable length of time, during a previous period. The fact that the total iron is greater at these depths seems to substantiate the postulate. Thus the high total iron at these depths may be explained as being due to very fine suspended particles that had previously existed in the water when it had approximate contact with the sea bottom.

The stations whose data are shown in Table V and Figure V are located on the continental shelf, off Cape Spencer, Alaska.

The soluble and total iron contents of the water collected over the continental shelf in the Gulf of Alaska are somewhat similar to those of the inland waterways, due to the marked turbulence of the waters in this region.

Conclusions.

1. A decided seasonal variation in the soluble and insoluble iron content of sea water has been observed. The minimum values occur in the spring and summer and the maximum in the winter.
2. A number of factors influence the distribution of the total iron.
3. The soluble and insoluble iron content of the open ocean is considerably less than that of coastal and inland waters.
4. A high total iron content occurs between 800 and 1100 metres, which is in the same zone where extremely low oxygen values were secured.

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Submarine Daylight and the Transparency of Sea Water.

By

Hans Pettersson.

THE supreme importance of submarine daylight as a basic factor in the maintenance of marine life was recognized long ago by eminent océanographers. In spite of the pioneer work of men like Fol and Sarasin, the Prince of Monaco, Helland-Hansen, Grein, and others, the experimental results obtained until ten years ago were scanty and mainly qualitative in character. Neither photo-chemical actinometers nor photographic plates lend themselves to accurate measurements.

Since 1923 W. R. G. Atkins and H. H. Poole (I) have applied photo-electric cells of the alkaline-metal type to measurements of subsurface illumination[1]). Thanks to their work the foundations of exact submarine actinometry have been established. Using an equipment of this type G. L. Clarke and his co-workers were able to measure the residual light at a maximum depth of 160 m. in the clear waters of the Sargasso Sea and have subsequently studied light penetration into the more turbid surface layers encountered in the Gulf of Maine and in the harbour at Woods Hole.

The low intensity of the photo-current from cells utilizing the external photo-electric effect necessitates the use at sea of amplifying sets, by means of which currents of 10^{-9} ampères and even less can be measured. This makes the equipment rather complicated in design, a fact which together with its cost seems so far to have deterred biologists from adopting the method, notwithstanding the valuable results it has been proved to give in the hands of trained experimenters.

The advent of the rectifying cell, where the internal photo-electric effect is utilized, has fortunately made submarine actinometry much simpler, owing partly to the more robust construction of these cells, partly to the much higher intensity of the photo-currents they yield

[1]) For papers published before 1932, *vide* W. R. G. Atkins's report in this Journal, Vol. VII No. 2, p. 171, 1932.

with illumination of a given brightness. Recently Poole and Atkins have published results from measurements made with the Bergmann-Weston cell in the English Channel. Pearsall and Ullycott have used Bernheim cells for light measurements in Lake Windermere, and Utterback and co-workers with the Bergmann-Weston cell have carried out extensive measurements on the penetration of nearly monochromatic components of daylight into the water of the North Pacific Ocean. In Sweden measurements of submarine daylight by means of rectifying cells were started early in 1933. At first cuprous oxide cells from Siemens & Halske were used but we soon went over to the selenium cells from Dr. B. Lange of Berlin-Dahlem (VII). Their chief advantage, besides their large yield, is the position of their spectral range of high sensibility, which comprises those parts of the spectrum to which coastal waters is most transparent.[1])

The main disadvantage of rectifying cells is the lack of linearity in the current/illumination relationship manifest with intense light of several thousand lux. The falling off in the photo-current with high intensities largely depends on the resistance in the cell circuit, as does also the temperature coëfficient of the cell. Both these disturbing factors are minimized by using a low-resistance instrument for measuring the photo-current. In most of our measurements we have been using a "light-spot" micro-ammeter from Siemens & Halske giving 1 scale-unit per 2.3×10^{-8} ampères, internal resistance = 18.4 ohms. With a special shunt giving constant resistance the sensibility may be reduced in the ratio from 1 : 3 down to 1 : 1000.

Another disadvantage of rectifying cells is a fatigue effect which also appears with intense light, the photo-current falling off with time by as much as 10 % or even more. With the latest type of cell submitted by Dr. Lange this effect is very small.

Since both the disadvantages just mentioned only appear with relatively intense light we have found it convenient when working near the surface in bright weather to cut down the intensity of the light incident on the cell by interposing a kind of optical sieve-filter made from perforated metal foil sandwiched between two discs of good opal glass. We have so far determined the transmission coëfficients of these filters by means of electric light, but are preparing an arrangement for measuring their transmission when immersed together with the cell to a depth of say ½ m., using diffuse daylight as source of illumination.

We have hitherto calibrated the cells, both dry and immersed in water, by means of standardized electric lamps. It is advisable to repeat such calibrations at intervals of a few months as a safeguard against any ageing effect possibly occurring in the sensibility of the cells. With the latest type of Lange cell this effect seems to be very small. It would be preferable to standardize the cells by means of daylight measured by means of an absolute actinometer. Thanks to

[1]) According to a communication from Dr. Lange the maximum of sensibility of his newest cells falls near 5750 Å, being 8 % less at 5250 Å.

the courtesy of Dr. Anders Ångström of Stockholm we hope in the near future to have our cells standardized in this manner. The absolute values of submarine illumination hitherto obtained in our measurements are therefore liable to the errors due to the differences in the spectral composition of light from high-temperature electric lamps and that of daylight.

The submarine actinometer.

The simple contrivance used by the author in collaboration with Mr. S. Landberg, 1st Assistant to Svenska Hydrografisk-Biologiska Kommissionen, for measuring submarine daylight and called by us the submarine actinometer is shown in Figure 1 reproduced from our

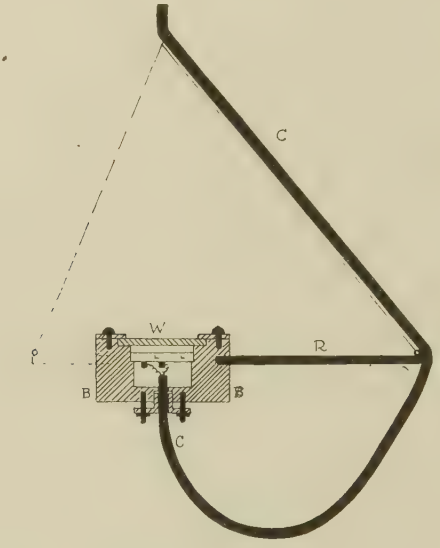

Fig. 1.
The submarine Actinometer.

preliminary reports. BB is a metal case made on the lathe from a cylindrical piece of brass 10 cm. in diameter and 5 cm. high. Below a strong glass window with roughened upper surface, W, the Lange cell L is exposed to daylight. The sieve-filter, when used, is inserted before the window. In our latest type of actinometer the electric cable enters the case from below, through a stout screw-piece, to the front of which the Lange cell is fixed. The instrument is suspended by three thin phosphor-bronze wires diverging from the instrument line and running to radial brass spokes screwed into the case. The rubber-insulated electric cable which carries the photo-current to the galvanometer on board the ship runs along one of the three wires so as to minimize its shadowing effect. The usual precautions against shadows from the hull of the ship are observed in the measurements.

With one of the Lange cells chiefly used in combination with the light-spot micro-ammeter an illumination of 1 lux produces a deflection of about 10 scale-units. In the open sea near our coasts the submarine daylight can in general be measured on clear days in the summer down to 60 m. depth or even more. But also with a less sensitive pointer galvanometer giving about 1 scale-unit per lux, the depth range of the instrument is quite sufficient for most purposes.

The submarine actinometer is very simple to use. Readings at different depths can be carried out very quickly. Reducing the photo-currents observed according to the varying intensity of the light incident on the surface, read on a deck-photometer with sieve-filter, we have found readings taken at the same depth, first with a descending and then with a rising instrument, to agree to within a few per cent., except near the surface where wave-motion and shadowing effects from the ship may cause larger discrepancies.

Besides ordinary measurements with the actinometer facing upwards, we have occasionally used two actinometers back to back, one for measuring the light from above, the other for the light scattered upwards. Again, in some measurements two actinometers facing upwards were carried by a frame at a fixed vertical distance, generally 2 m. apart, so that the extinction suffered by the daylight in a water column of the same height could be compared at different depths. Finally two actinometers, one above the surface of the Gullmar Fjord, the other one suspended at a depth varying with the season and the turbidity of the surface water, have been used for more than a year in combination with a recording galvanometer for continuous registration of submarine daylight. The records, which were at times obtained below an ice sheet 20 cm. thick, will be dealt with together with other actinometric results in a separate publication now being prepared.

As an example of further use to which the submarine actinometer has been put at our research station at Bornö, an investigation may here be alluded to which was carried out during the spring increase of diatoms in 1934 by the author in collaboration with Mr. L a n d b e r g and Mr. H. H ö g l u n d, plankton specialist to our Kommission. Spherical glass flasks of special construction containing raw diatom cultures were mounted at the ends of horizontal arms from a brass stand. The latter could be kept in movement along a slanting wire running down from the platform before Bornö Station to a piece of rock on the bottom of the fjord. To one arm of the brass stand a submarine actinometer, facing upwards, was attached. The whole arrangement was kept moving while the experiment lasted, so as to keep the photo-current from the actinometer at a constant value, thus allowing the diatoms to carry on their photosynthesis in daylight of constant intensity. The oxygen produced in the flasks compared with that from controls wrapped in black cloth was measured according to W i n k l e r. The purpose of the experiments was to find the „compensation intensity" of daylight which is required for making oxygen

production through photosynthesis just balance oxygen consumption through respiration. As an approximate value for the compensation intensity with raw cultures of the kind used, not free from metazoans, we found 400 lux. The investigation will be resumed during the spring increase of 1935 on a more extensive scale and under improved experimental conditions.

The transparency of sea water.

A beam of parallel monochromatic light passing through a column of optically pure sea water x metres in length becomes reduced in intensity from an initial value I_o according to the exponential equation

$$I_x = I_o\, e^{-x\mu_w} \qquad (1)$$

where e, $= 2.71$, is the basis of natural logarithms. The exponent μ_w is generally called the absorption coëfficient, although part of the loss is due to scattering against water molecules, salt molecules and ions[1]). It is independent of x but varies considerably with the wave-length of the light.

If the water contains suspended particles a further loss in intensity is caused through scattering against the particles and to some extent also through absorption in them. This loss can also be assumed to vary according to an exponential law[2]), so that the compound loss will be given by the equation

$$I_x = I_o\, e^{-x(\mu_w + \mu_p)} = I_o\, e^{-x\mu} \qquad (2)$$

whereas the first term in the exponent, here for convenience sake called the "coëfficient of water-extinction", is due only to the water itself and the dissolved substances it contains; the second term is due to the suspended particles and may be called the "coëfficient of particle-extinction". The sum of these two coëfficients will here be called simply the "extinction coëfficient". Provided the geometrical and optical properties of the particles and also their number per unit volume are the same throughout the column μ_p will be independent of x with monochromatic light but will vary with the wave-length. With daylight as well as with artificial light the compound extinction coëfficient in Equation 2 will necessarily vary with x and will decrease with increasing values of x, since those light-components which are most strongly absorbed or scattered will to an increasing degree become filtered away as the length of the column increases, leaving the residual light relatively rich in the more penetrating components.

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[1]) According to Hulburt, J. Opt. Soc. America, Vol. XII, p. 408, 1932, the energy lost through Raman scattering in sea water does not exceed 25 % with any wave-length investigated and is generally considerably less.

[2]) Compare Lord Rayleigh, Collected Papers, Vol. IV, p. 109, Cambridge Univ. Press.

For practical purposes it is convenient, as Atkins and Poole have done, to define the rate at which daylight penetrating downwards into the sea has its intensity reduced by the equation

$$I_h = I_o \, e^{-h\mu_v} \qquad (3)$$

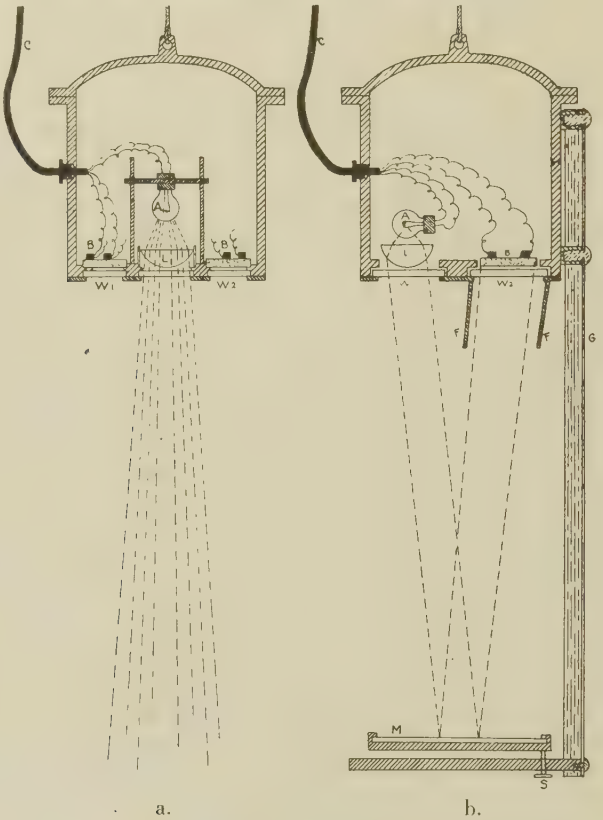
where I_o and I_h are the intensities of the daylight incident from above at the upper and lower end of a vertical column of sea water h m. in length. The coëfficient μ_v is here called the "vertical extinction coëfficient"[1]). The numerical value of this coëfficient must be expected to vary with the length of the column and with the depth at which it is situated, partly for reasons already stated, partly because the path of the light rays, which are mostly oblique, will exceed *h* in a degree which increases with increasing depth as the daylight gets more diffuse in character.

Values of the vertical extinction coëfficient have hitherto been found from measurements of submarine daylight at consecutive depths from which values of μ_v have been calculated for the intervening water columns. There are several disadvantages inherent in this method. Owing to the progressive change in spectral composition which daylight undergoes with increasing depth, the values found for μ_v in different depths are not comparable *inter se*. Thus with water of perfectly constant optical properties from surface to bottom quite different values for μ_v will be found near the surface and at greater depths. By measuring the intensity of narrow spectral bands, cutting out the other components of daylight by means of optical filters, as Utterback and Jorgensen have done, comparable values for μ_v are obtained, but only at the cost of a very large reduction in intensity, necessarily limiting severely the depth to which such measurements can be carried out. Apart from this restriction the occasions at which such observations are feasible are limited to daytime with a fairly strong light, i. e., they are limited by the season, the latitude, and the meteorological conditions. Finally all errors inherent in daylight measurements, such as are caused through wave-motion, shadowing effects, etc., enter twice into the values calculated for μ_v.

On the other hand, the transparency of sea water, apart from its significance for subsurface illumination, has an interest of its own. Experience has shown that the very considerable variations in transparency encountered are largely if not exclusively due to the presence in the water of suspended particles, i. e. μ_p in Equation 2 varies, whereas μ_w remains very nearly constant. In many cases the majority of the particles causing these variations are organic, either

[1]) Since the extinction is a compound process involving both true absorption and scattering the name of "absorption coëfficient" for μ is obviously a misnomer. On the other hand, "extinction coëfficient" appears preferable to "transmission coëfficient" since a high value of μ corresponds to a strong extinction but to a low transmission and *vice versa*.

organic detritus or living plankton organisms. Transparency measurements carried out by an accurate method might, therefore, afford means of finding the depths where such particles are specially abundant, perhaps also of estimating approximately their amount.



a. b.

Fig. 2.
a) Scattering Meter. b) Transparency Meter.

The transparency meter.

In order to measure the transparency of sea water to a beam of artificial light of constant initial intensity and spectral composition, the transparency meter, abreviated to T. M., shown in Figure 2 (b), has been constructed. A cylindrical casing with flanges, closed hermetically by means of a lid with interposed rubber washers, is made from cast brass, chromium-plated externally against corrosion. Two circular windows *W* made from thick plate glass are inserted into round apertures through its bottom. Over one of the windows an electric lamp *A* is mounted behind a hemispherical glass lens *L*, so that a slightly diverging cone of light is projected out into the water through the window. At a distance of 1 metre from the window the beam is reflected back by a plane mirror, held securely by three strong

L-girders made from stainless steel fixed to the brass casing. The reflected beam passes through the second window on to the Lange cell *B*. A narrow metal funnel *F*, before the second window serves to keep back diffuse daylight as well as light scattered backwards from the descending beam of light. Water can circulate freely between windows and mirror. Using the T. M. near the surface in daytime an extra cylindrical screen round the upper parts of the girders serves to reduce the effect from diffuse daylight on the cell. By means of two wires in a 4-wire rubber-insulated electric cable *C* the lamp is fed with current from a battery of storage cells, adjusted by means of a rheostat and measured by a precision ammeter on board the ship. The other pair of wires carry the photo-current to the micro-ammeter; generally the light-spot instrument was used.

Before immersing the instrument the lamp-current is regulated so that the photo-current produced by the beam of reflected light gives a deflection covering nearly the whole scale, say 140 units out of 150 possible. At each measurement in the immersed condition the lamp-current must be adjusted to exactly the same strength. The photo-current observed in daytime near the surface without lamp-light, generally a few scale-units only, has to be deducted from the readings at the same depth taken with the lamp burning.

The T. M. was first used in the position indicated in the figure, i. e. with the light beam projected downwards, thus giving the average transparency within a vertical column of 1 m. Experience having shown that even within this length the optical properties of sea water may change by as much as 50 % or even more, we have taken to using the instrument in a horizontal position. The transparency within a water layer only some 15 cm. thick can be measured in this manner.

Two sets of readings, one made with a descending, the other with an ascending instrument, nearly always agree to within a few per cent., exceptions occurring at so-called "optical boundaries" where the transparency varies very rapidly with the depth. By lowering the instrument with the lamp burning and observing the photo-current, even small changes in the optical properties of the water can be localized. The instrument is both easy to manipulate and quick to work with. Since the relative variations in transparency with depth are of particular interest we have generally taken the photo-current read at each depth, corrected for daylight effects, as a measure of the transparency. It will be seen from the following that even with this arbitrary measure results of interest are found. An approximate value for the extinction coëfficient of the water between windows and mirror can, however, be calculated in the following manner:

Having measured the "deflection in air" S_a under standard conditions we may calculate an approximate value for the deflection S_i which should be found in water of ideal optical properties, i. e. where μ_w and μ_p are both vanishing[1]). Assuming the light intensity over

[1]) It would be of considerable interest to standardize the T. M. in optically pure sea water perfectly free from suspended particles, which would make it possible to

a cross-section through the beam at right angles to its axis to be constant, the intensity compared to that in air ought to increase as $1/n^2$ owing to the contraction of the beam in a medium of the refractive index n. A further increase of about 10 % would ensue from reduced losses through reflection at the glass/water surfaces. In all we should have very nearly $S_i = 2\ S_a$, and hence the deflection actually found in water of the extinction coëfficient μ becomes

$$S_w = 2\ S_a\ e^{-2d\mu} \qquad (4)$$

where d is the distance between window and mirror. Generally $d = 1$ metre. A very accurate value for μ cannot be calculated from Equation 4 for the reason that the light intensity across the beam is not perfectly uniform, as was here assumed.

Measurements with the T. M. can be carried out at any time of the day or night independent of daylight and also beneath an almost opaque surface-layer such as one often encounters in the fjords after heavy rain. In fair weather the transparency can be measured immediately below the surface and down to depths limited only by the length of the cable and the strength of the casing and especially of the windows. Hitherto we have not worked the T. M. at greater depths than 85 m. but we hope to be able to use a new instrument of more robust construction down to 500 m. depth, if not more.

It should be pointed out that, owing to the difference in spectral composition between the artificial light used with the T. M. and daylight one cannot expect any close agreement between the values of μ found from Equation 3 and such values for μ_v as are calculated from daylight measurements. On the other hand the former results will be largely free from the errors in μ_v which are due to the changes daylight undergoes with increasing depth. Their chief importance lies, however, in the information they give regarding the suspended particles present in different water strata[1]).

The scattering meter.

If the assumption made above were true, viz., that variations in transparency with the depth such as are revealed by the T. M. are really due to scattering against particles suspended in the water, one would expect these variations to be accompanied by similar variations, but of opposite sign, in the amount of light scattered backwards from a strong beam of light projected into the water. In order to test this point the instrument shown in Figure 2 (a), here called a scattering meter (for convenience sake abreviated to S. M.), was constructed. Its function is made clear by the figure alone. Suffice it to say that

calculate values for the coëfficient of extinction by particles, μ_1 in Equation 3. A container suitable for such measurements is at present being built for Bornö Station.

[1]) After completing this MS. I find that an ingenious method for measuring the transparency of lake-water near the surface by means of artificial light was used in 1928 by S. G. Hibben. Trans. Illumin. Soc. Amer. Vol. XXIII, p. 959, 1928.

since the fraction of light scattered backwards by particles in the water is very much smaller than the fraction reflected against a mirror, both the intensity of the light and the sensibility of the arrangement for observing the photo-current had to be considerably increased. The lamp used was an automobile headlight lamp of 50 c. p. from which

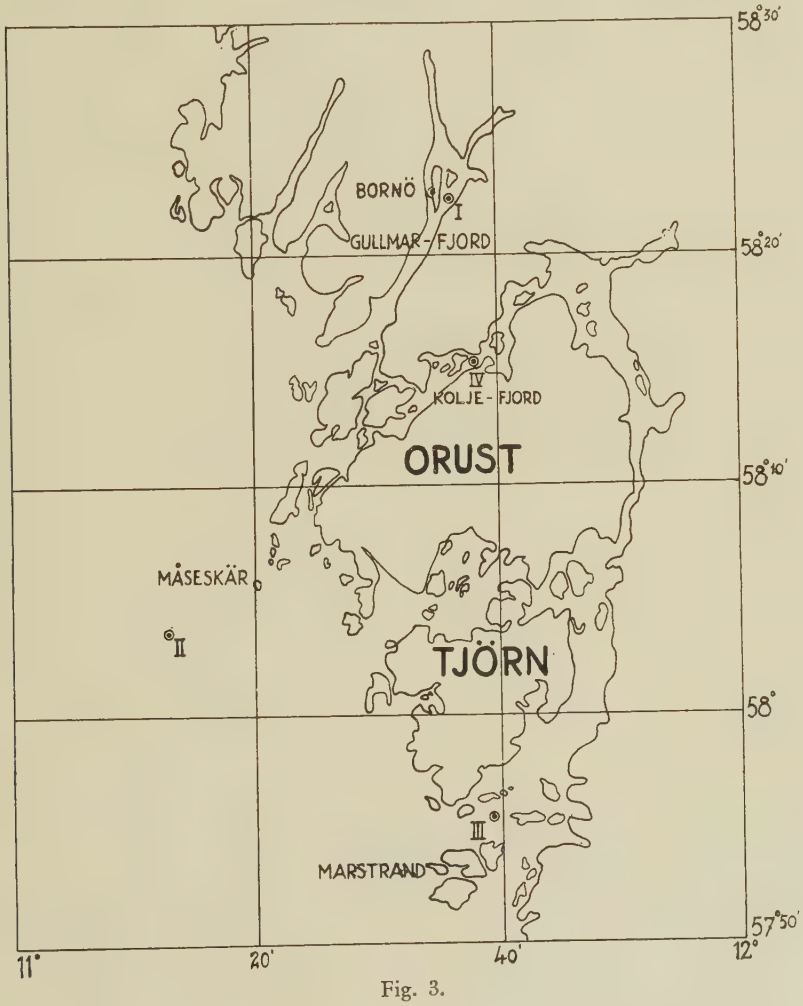


Fig. 3.

a strong beam, made slightly divergent by means of a lens, was emitted through a central window. The Lange cells were 4 to 6 in number and were exposed to the scattered light behind peripheric windows in the bottom of the casing. Otherwise the S. M. closely resembles the T. M.; in fact the casing for our newest instrument is made with several windows, so that they can be used for either purpose, with and without a mirror. In use the S. M. is as simple as

the T. M., save that it requires a much stronger lamp-current and cannot be used near the surface by day. Like the T. M. it gives more concise results suspended horizontally than vertically.

The Results.

From the first the results obtained with the T. M., in the autumn of 1933, proved its indications to be consistent *inter se* and to reveal pronounced variations with depth in the transparency of coastal waters, which variations appeared to be related to the abundance of organic detritus and of plankton organisms in the water (XII). Thanks to the ready assistance from Mr. H ö g l u n d it was possible, during the spring increase of diatoms in the Gullmar Fjord in 1934, to coordinate such variations in transparency and in scattering with the number of cells present in the water at different levels. A sharp fall in the transparency and an equally sharp rise in the scattering were found to occur just below a very steep rise in salinity, marking the boundary between a surface layer of Baltic water and an underlying layer of salter "bank-water". The optical boundary, which was thus found nearly to coincide with the salinity boundary, was also characterized as a biological boundary, the number of plankton organisms, largely diatoms, being there much higher than in either the lower or the upper levels (XIII).

Late in the autumn of the same year we had again facilities for making such measurements from the "Skagerak" both in the Gullmar Fjord and in some neighbouring localities, the most important of which are denoted by the Roman figures I to IV in the map reproduced here as Figure 3. The first of these series, taken at Ormestad near Bornö, gave an example of conditions where transparency measurements with daylight would have been of little value.

Owing to unusually heavy rains the Gullmar Fjord had for several weeks been covered with an almost opaque surface-layer of brownish water containing clay particles from the small rivers and brooks discharging into the fjord. Daylight measurements made with the submarine actinometer on an almost clear afternoon (Oct. 30th) proved that subsurface light at a depth of ½ m. was already reduced in intensity to a small fraction of its value in the uppermost surface, 900 lux compared to 8,000 lux. In 5 m. depth the intensity had become further reduced to 18 lux, and at 20 m. the residual light, being only a fraction of 1 lux, could not be accurately measured. See Columns 2 and 3 of Table I.

The results from measurements with the T. M. and the S. M., both vertical, are set out in graphs in Figure 4. Thanks to the turbid surface-layer they were carried out without any complications from daylight. Only just below the surface no accurate readings were made, since the T. M. there gave no observable photo-current, whereas with the S. M. the deflection was excessively large, the cone of light appearing reddish in colour. At all other depths, as far as the cables reached, the

Table 1.

Station I Lat. 58° 22½′ N.; Long. 11° 37′ E. depth 84 m.					Station II Lat. 58° 4½′ N.; Long. 11° 13½′ E. depth 65 m.				
Depth	daylight		transparency		Depth	daylight		transparency	
	lux	μ_v	scale-units	μ		lux	μ_v	scale-units	μ
0.5	900	—	0	—					
0.8	—	—	8	1.78					
1	256	2.52	19	1.35	1	400	—	30	1.21
2	74	1.24	36	1.04	2	225	0.56	45	0.91
3	47.5	0.44	79	0.64					
4	28.0	0.53	88	0.59					
5	18.0	0.44	100	0.53	5	110	0.24	102	0.41
7	7.1	0.47	105	0.50	7	164	0.26	112	0.46
10	2.6	0.34	108	0.49	10	33	0.22	120	0.42
					12.5	21.5	0.17	121	0.42
15	0.7	0.26	122	0.43	15	15.7	0.17	121	0.42
20	0.2	0.27	121.5	0.43	20	6.8	0.17	121	0.42
22.5	—	—	102.5	0.51					
24	—	—	88	0.59	25	3.5	0.13	123	0.41
25	—	—	91	0.58					
26	—	—	111.5	0.42					
30	—	—	124.5	0.42	30	2.2	0.09	121	0.42
35	—	—	123.5	0.42	35	1.5	0.08	113	0.45
38.5	—	—	105.5	0.50					
40	—	—	113	0.46	40	1.2	0.05	115	0.44
45	—	—	131.5	0.39	45	—	—	114	0.45
50	—	—	134	0.38	50	—	—	101	0.51
55	—	—	131	0.39	55	—	—	85	0.60
60	—	—	143.5	0.35	60	—	—	82	0.61
65	—	—	133	0.38					

observations were made without any difficulty and gave quite consistent results.

The trends of the transparency and the scattering curves are seen to be beautifully antisymmetrical, proving that the main variations in the extinction are in fact due to scattering. There is a sharp minimum in transparency at 24 m., a maximum between 30 and 35 m., and a second minimum near 38 m. Owing to shortness of the cable used with the S. M. the scattering curve does not go further down than to 38¼ m.

The continuous line curve shows how the density varied with the depth. There is a sharp rise between 15 and 20 m. followed by a less steep rise between 20 and 25 m. The optical boundary is in this case seen to coincide with the lowest part of the density boundary.

Plankton samples were taken at four depths, viz. at 22, 24, 26 and 40 m. and were analyzed by Mr. H ö g l u n d according to the sedimentation method of U t e r m ö h l. The figures, set out within circles in the figure, show that the greatest number of organisms, over 60,000 diatom cells per litre, was present in the optical boundary at 24 m., whereas only 2 m. higher up, the number was 40 % less and

2 m. further down, it fell 15 % short of the maximum value. At 40 m. depth, near the secondary minimum in transparency, the number of organisms was quite small. The particles causing this minimum must, therefore, be assumed to be detritus, either organic or inorganic in nature.

Table I gives in its 3rd and 5th columns the values of the compound extinction coëfficients, μ_v calculated from daylight measurements according to Equation 3 and μ from transparency measurements according to Equation 4. In the daylight column the figures were calculated for

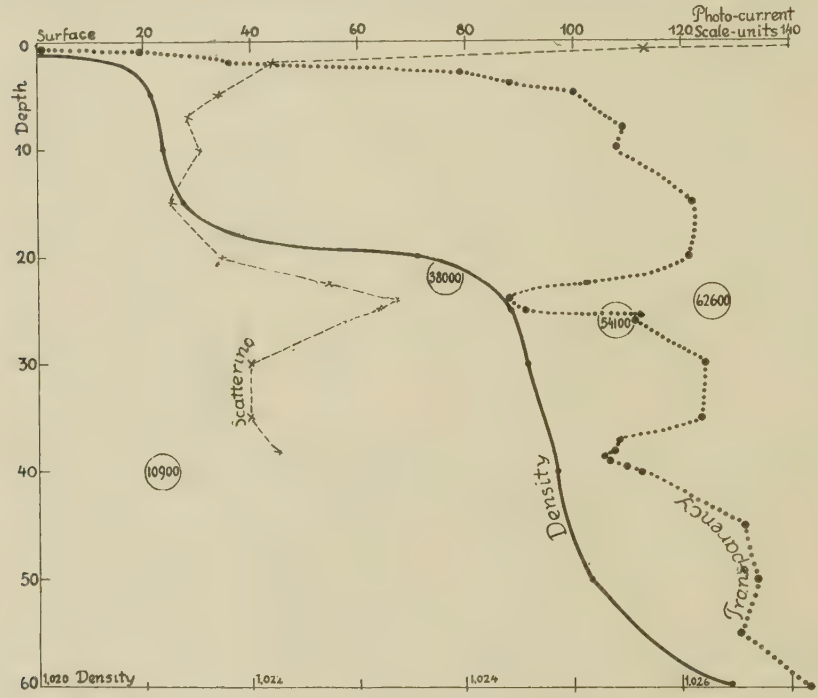


Fig. 4.

columns between two consecutive depths, in the transparency column the figures refer to a water layer extending by ½ m. above and by as much below the figure given as depth. The values of μ_v and μ are seen not to differ so very much near the surface, whereas in greater depths the daylight figures are distinctly smaller than those found with artificial light. That the discrepancies between the two columns are not still larger in these depths is, no doubt, due to the fact that daylight has already lost its short-wave components, which in clear water are the most penetrating, in the turbid surface-layer, so that its spectral composition resembles that of the electric light much more than what would have been the case under a clear surface-layer. The interesting changes in transparency between 20 and 40 m., revealed by the T. M. and the S. M., were beyond the reach of daylight observations.

An abbreviated series of measurements was made outside the coast line at the locality marked II in the map, two days afterwards. Here the surface water was much less turbid, so that daylight measurements by means of the submarine actinometer could be extended to a depth of 40 m. on an overcast afternoon (Oct. 31st). The results as well as the values of μ_v calculated therefrom are set out in the second part of Table I, Columns 7 and 8. The last two columns of the table give the

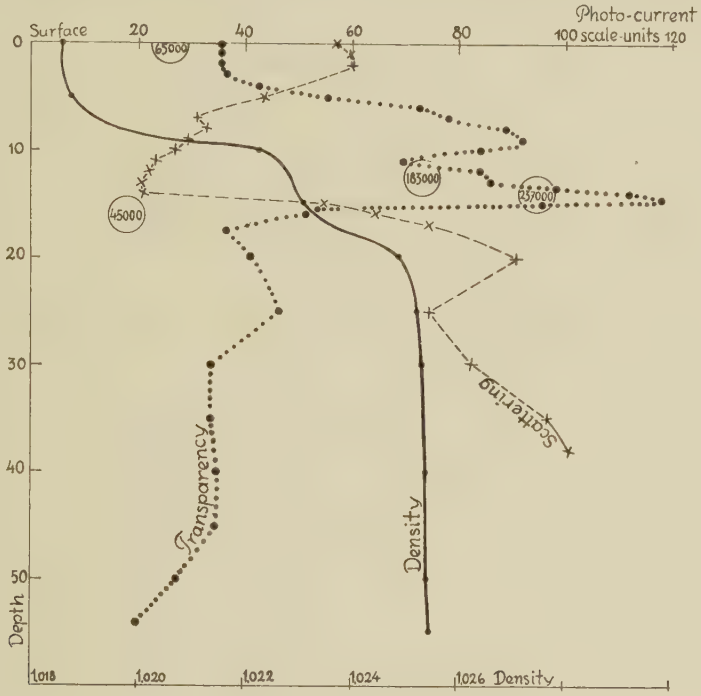


Fig. 5.

results from transparency measurements which were carried out almost down to the bottom at 63 m. The transparency is seen to have a faint maximum at 25 metres but otherwise does not show any variations of interest. It should be added that the water was of almost uniform density from 5 m. down to the bottom and only slightly less dense at the surface. In this case the discrepancies between the extinction coëfficients found with daylight and with artificial light are much larger than at Ormestad. The values of μ are seen to vary very little with the depth between 7 and 40 m. whereas μ_v within the same depth range falls to less than one-fifth. There is little doubt that the latter change is not at all due to any change in the transparency of the water but instead to the progressive change in the composition of daylight already mentioned.

On the following night the measurements set out in graphs in Figure 5 were made at the locality marked III in the map, which is situated at the very entrance to the sequence of narrow fjords encircling the large islands of Orust and Tjörn. Here an interesting situation is revealed, which appeared at first to contradict the conclusions inferred from previous measurements. Here also the curves obtained with the T. M. and with the S. M., the former instrument used for the first time in a horizontal position, are seen to be antisymmetrical. The minor discrepancies found in the curves may be explained as due to the difference in their position, T. M. horizontal, S. M. vertical. Both curves show a strong maximum in transparency, a minimum in scattering, at 14½ m. and the reverse between 17½ and 20 m. The minimum in transparency at 17½ m. may be associated with the rise in density occurring near that depth, whereas there is a secondary minimum in transparency at 10 m. which we may attribute to the sharp rise in density occurring between 5 m. and the latter depth.

Plankton counts revealed the surprising fact that a maximum of organisms, in itself not very high, 237,000 cells per litre, was found in the very clearest water at 14¼ m. whereas at 12½ m. the number found was 183,000 and both in the surface and at 16 m. very much less, 65,000 and 45,000 cells per litre respectively. Mr. H ö g l u n d observed, however, that in the clear water at 14¼ m. there was almost no organic detritus present, the three other samples containing quite large amounts of it. This subjective estimate has since been confirmed through a more quantitative test, developed by Mr. H ö g l u n d, in which micro-photographs taken from U t e r m ö h l's sedimentation cylinders containing samples from the different depths considered are compared. These and other micro-photographs bearing on the same question will be published shortly in a separate report.

Finally in Figure 6 ar given graphs from measurements made in the innermost of the fjorc before mentioned, Kolje Fjord, marked IV in the map. Again the conditions are seen to differ considerably from those found three days earlier in the Gullmar Fjord. There were comparatively few clay particles in the surface water, which was, instead, turbid from the enormous amount of diatoms it contained. Over 3 million cells per litre were found both in the surface and at 5 m., whereas in the deeper layers there was but little plankton present. The density of the water shows a steep rise from 9 to 10 m. and a more gradual increase between the latter depth and 20 m. The transparency and scattering curves have the usual antisymmetrical trend; both instruments were here used in a horizontal position. There is a sharp rise in transparency below the surface-layer rich in plankton, i. e. from 5 to 10 m., and series of minor maxima and minima at lower depths, which cannot be explained as due to plankton organisms, but are instead probably caused by organic detritus. This point could not be ascertained by the micro-photographic method for lack of a sufficient number of samples.

Measurements similar to those here described have subsequently

been made both in the fjords and in the open sea. The results confirm those here set out. The curves obtained with the T. M. and with the S. M. are antisymmetrical and their maxima and minima, as far as the experimental evidence hitherto examined goes, are to be explained as chiefly due to inorganic particles in the surface and to organic particles at lower depths. Distinct minima in transparency are often, but not always, localized in or just below density boundaries. In the Gullmar Fjord there is in general a minimum of transparency near 40 m. (the threshold depth at the entrance), whereas the most transparent secondary layer is generally found at 60 m. in the upper part of the more stagnant water filling its deeper basin.

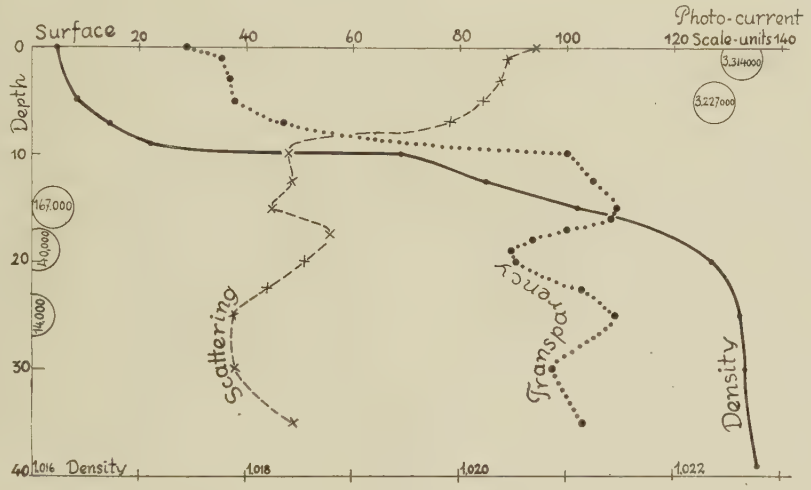


Fig. 6.

Discussion.

The results here related show that both the T. M. and the S. M. allow of a rapid survey of the optical properties of sea water *in situ*. There is no doubt about the reality of the variations in transparency thus revealed, nor of their origin, which is mainly if not exclusively scattering against the particles suspended in the water. These particles, again, are found to accumulate at certain depths, here denoted as optical boundaries, which are often associated with the density boundaries characteristic of stratified water.

From optical measurements alone it is not at present possible to decide whether the particles causing the scattering of the light are organic or inorganic in nature. Experiments now being undertaken, in which colour filters are inserted before the Lange cells, will perhaps afford means for a discrimination between the two kinds of particles since, owing to the difference in size between them, they should be

expected to affect light of different wave-lengths to a different degree. There are, on the other hand, reasons for assuming the particles accumulated at some depth below the surface, and especially near density boundaries, to consist of organic matter, since the very small excess in the specific weight of such particles over the density of sea water will make their sinking velocity through water layers of different density much more dependant on the latter than that of inorganic particles, which have a density at least double that of the water. This reasoning lends further support to the conclusion inferred from Mr. Höglund's plankton counts and micro-photographic method for estimating the amount of organic detritus, viz., that optical boundaries found near density boundaries are due to clouds of organic matter.

That organic matter tends to accumulate in the transition layers in the open ocean, characterized by a rise in either density or viscosity (or both), has long been recognized. Thus, the late Sir John Murray considered one of the most important results from his joint expedition with Dr. Johan Hjort on board the "Michael Sars" in 1910 to be their observations on the "feeding ground" for pelagic fishes encountered in the North Atlantic Ocean between 200 and 400 m., which is caused by an accumulation of sinking plankton organisms from the surface. It appears that a similar accumulation, only much more pronounced in character, occurs with neritic plankton organisms and organic detritus near the density boundaries in coastal water. The changes in level which these plankton-rich layers are apt to undergo through the internal movements occurring in the water will affect the intensity of the daylight they receive and consequently influence also the rate of their photosynthesis.

Another fact brought out by these measurements is the dominant influence on subsurface illumination and necessarily also on the productivity of phytoplankton exerted by a turbid surface-layer, such as in a rainy season may persist for many weeks in the fjords, retarding and reducing the development of the diatom vegetation.

It seems therefore that in order to extend our knowledge of the production of organic matter in coastal waters by phytoplankton and by macroscopic algae, both the light factor and the internal movements will have to be closely studied, a study which, from a technical viewpoint, is now within the reach of biologists no less than of oceanographers.

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Einige Ergebnisse von Beobachtungen an *Clupea harengus* des Barentsmeeres.

Von

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DA ich meine Untersuchungen an *Clupea harengus* des Barentsmeeres unterbrochen habe und kaum gedenke, sie später wiederaufzunehmen, so halte ich es für angebracht, einige der ermittelten Befunde mitzuteilen.

Makuschok hat einen grösseren Aufsatz veröffentlicht (Arbeiten des Staatlichen Ozeanographischen Instituts (russisch abgefasst, Bd. I, Lief. 4, 1932), in dem er durch Analyse der Beobachtungen verschiedener Verfasser zu beweisen trachtet, dass es eine besondere *Clupea harengus*-Rasse des Barentsmeeres gibt, der ein bestimmtes Wohngebiet an der Murmanküste zukommt. Ebenda sollen sich, laut Makuschok, auch die bisher unbekannten Laichplätze besagter Rasse befinden.

Obzwar ein solcher Standpunkt sehr verlockend ist, so kann ich mich ihm dennoch nicht anschliessen, zumal es keine einzige wirklich unbestrittene Tatsache gibt, die den Nachweis des Bestehens einer Murmanrasse von *Clupea harengus* ergeben würde. Meine diesbezüglichen Forschungen lassen sich kurzgefasst folgenderweise darstellen: Bisher werden im westlichen Teile des Barentsmeeres, d. h. westlich von dem Eingang in das Weisse Meer, sowohl unmittelbar an der Küste wie auch fern von derselben in grossen Mengen junge, unreife *Cl. harengus* angetroffen oder solche, deren Gonaden sich in den ersten Stadien der Reife befinden. Exemplare, die vor dem Fange, wenn auch nur ein einziges Mal, gelaicht hätten, habe ich noch nie zu sehen bekommen. Ausnahmsweise, und das auch nur sehr selten, kommt eine geringe Zahl von Exemplaren, vorwiegend Männchen, vor, deren Gonaden der Reife nahe sind. In fast allen Fällen, in denen das Alter der hier erbeuteten *Cl. harengus* bestimmt wurde, erwiesen sich die Fische als nicht über 4 Jahre alt; mitunter kamen auch fünfjährige und noch viel seltener sechsjährige vor. Siebenjährige und noch ältere

Exemplare sind bis jetzt im erwähnten Gebiete des Barentsmeeres nicht beobachtet worden.

Vor einigen Jahren hat Rabinerson (Bulletin de la Section de l'Ichthyologie pratique [russisch] Bd. III, Lief. I, 1925) bei Erforschung einer geringen Zahl von in den Fjorden der Murmanküste erbeuteten *Cl. harengus* diese als Jungfische der norwegischen Rasse gedeutet. Später hat Borodatowa (Zool. Anz. Bd. 84, H. 11/12, 1929) an der Hand des Bestehens einer ziemlich starken Divergenz zwischen dem Wachstum der von ihr erforschten murmanschen *Cl. harengus* und den typischen norwegischen Heringen, die sich besonders scharf im Laufe des 2. und 3. Lebensjahres der Fische kundgibt, und sich auch nach der Differenz in der Wirbelzahl (Vert. S. und Caud. Vert.) richtet, geschlossen, dass der Murman-Hering von dem norwegischen verschieden ist.

Das noch unveröffentlichte Material von N. Ssytsch-Awerinzewa, das sich auf im Winter 1932/33 in den Fjorden der Murmanküste erbeutete *Cl. harengus* bezieht, zeugt dafür, dass die prozentuale Häufigkeitskurve des Merkmals Vert. S. verschiedener Proben grosse Ähnlichkeit miteinander sowie mit einer analogen, nach Rabinersons Angaben dargestellten Kurve aufweist. Es ist von grossem Belang, dass während der zehn Jahre, die zwischen der Erbeutung der Proben Rabinersons und derjenigen von Ssytsch-Awerinzewa verflossen sind, bei den murmanschen *Cl. harengus* keine wesentlichen Veränderungen in der Verteilung der Wirbelsumme stattgefunden haben. Durch Vergleich der besagten Häufigkeitskurven (Vert. S.) mit den Kurven, die Runnström für einige Proben der der 0-Gruppe angehörenden *Cl. harengus* aus den nördlichen Gebieten Norwegens anführt (Journ. du Conseil, Vol. VIII, No. 2, 1933, Abb.4), lässt sich eine grosse Ähnlichkeit zwischen diesen und jenen aufdecken. In den Proben von Ssytsch-Awerinzewa schwankt der Durchschnittswert für Vert. S. zwischen 57.16 und 57.34 (wobei σ 1.17 — 1.29 beträgt). Dem Alter nach gehören die *Cl. harengus* dieser Proben in einigen derselben vorwiegend der I-Gruppe, anderen der II-Gruppe an, und nur in wenigen Proben kommen der III-Gruppe angehörende Exemplare, zusammen mit solchen der IV-, V- und VI-Gruppen vor.

Ich habe feststellen können, dass Exemplare der 0-Gruppe in den Buchten des Motowsky Golfes, und auch weiter ostwärts, bis Teriberka (möglicherweise auch noch östlicher), in der ersten Hälfte des August vorkommen.

Beim Vergleich der hier aufgezählten Tatsachen mit dem, was über die Laichgebiete, die Art und Zeit der Verteilung der Jungfische an der Küste Norwegens, sowie über andere charakteristische Besonderheiten der norwegischen *Cl. harengus*-Rasse aus den vorzüglichen Arbeiten Einar Leas und, in den letzten Jahren, aus den Arbeiten Runnströms bekannt geworden ist, muss meines Erachtens unumwunden der Schluss gezogen werden, dass die Murman-Heringe als Jungfische der norwegischen Rasse zu deuten sind, die vom Strom

weit nordostwärts getrieben worden sind und die dann während ihrer ersten 4—6 Lebensjahre sich an der Murmanküste aufhalten. Als Laichgebiet kann für diese *Cl. harengus* nicht bloss die Stadt—Kristiansund Region (Möre-Küste) sein, sondern hauptsächlich die Lofoten—Vesterålen Region.

Es ist zu vermerken, dass bei der Untersuchung der Schuppen solche vom Nord- wie auch vom Südtypus (nach L e a s Terminologie), also solche mit scharf ausgeprägten und umgekehrt mit verschwommenen Winterringen vorgefunden worden sind. Schuppen des letzten Typus machen 15—20 % oder noch weniger aus.

Meines Erachtens ist die Möglichkeit nicht ausgeschlossen, dass unter den Murman-Heringen Exemplare vorkommen können, die den Formengruppen angehören, welche, gemäss der Terminologie P. B j e r k a n s, als "landlocked" gedeutet werden dürften (Rapp. et Proc.-Verb., Vol. LXV, 1930); prozentual muss ihre Zahl jedoch dermassen gering sein, dass ihr Vorkommen unsere Schlussfolgerung bezüglich der Herkunft von *Cl. harengus* des westlichen Teiles des Barentsmeeres keineswegs beeinträchtigen kann. Als ich 1923—1926 die Heringe des Weissen Meeres untersuchte, habe ich (Wiss. Meeresunters. Bd. XV, Festschr. F r. H e i n c k e) unter einer Gruppe von Rassen mit gleicher Wirbelzahl, die im Durchschnitt 53—54 betrug, und die als der *Cl. pallasi* des Pazifischen Ozeans verwandt zu betrachten ist, auch noch eine Rasse mit einer durchschnittlichen Wirbelzahl von 57.12—57.20 vorgefunden.

Da es nicht gelungen ist, unter den Vertretern dieser Form geschlechtsreife Exemplare aufzufinden, so habe ich die Exemplare, die nur zeitweilig, und zwar im frühen Alter, das Weisse Meer bewohnen, als ozeanische *(Cl. harengus)* Rasse bezeichnet. Nach 1924—25, als ich zum ersten Male einzelne Scharen dieser *Cl. harengus*-Rasse getroffen hatte, haben sowohl ich wie meine Mitarbeiter dieselben mehrmals im Weissen Meere vorgefunden. Ebensolche unreife Heringe sind auch S s y t s c h - A w e r i n z e w a (1933) in den Proben aus dem Mesen-Fjord des Weissen Meeres zu Gesicht gekommen. Ein Vergleich der prozentualen Häufigkeitskurven des Merkmals Vert. S. besagter Formen aus dem Weissen Meere und der murmanschen *Cl. harengus*, sowie auch die Analogie ihres Wachstums weisen auf völlige Identität dieser beiden hin. Also gelangt eine gewisse Menge junger, unreifer (den 0- und I-Gruppen zugehöriger) norwegischer Heringe in das Weisse Meer, indem sie die Küste der Kola-Halbinsel entlang ziehen, und kehren an der Küste der Halbinsel Kanin entlang in das Barentsmeer zurück. Diese norwegischen *Cl. harengus*-Rassen halten sich im Weissen Meere nicht länger als 1—2 Jahre auf.

Das Gebiet des Einganges in das Weisse Meer teilt das Barentsmeer, in betreff der Verteilung der Heringsrassen, in zwei Teile, den östlichen und den westlichen Teil. Der letzte ist bereits besprochen worden. Im östlichen kommen, wie aus den unveröffentlichten Befunden von S s y t s c h - A w e r i n z e w a zu ersehen ist, Exemplare vor, deren mittlere Wirbelzahl der Zahl 54 nahesteht, die also der Hauptgruppe

der Heringe des Weissen Meeres *(Cl. pallasi)* verwandt sind. Es kommen diese Formen im Tscheschskij Golfe vor, wo sie Ende Mai — Anfang Juni laichen, dann an der Mündung des Flusses Petschora, bei der Insel Kolgujew und weiter ostwärts bis an die südlichen Golfe des Karischen Meeres. Die Heringe sind hier (mit Ausnahme des Karischen Meeres) durch eine einzige Rasse mit etwas unbeständigen Merkmalen vertreten (ebenso wie die Merkmale der norwegischen *Cl. harengus*-Rasse variabel sind). Gemäss ihrer maximalen Körperlänge wie auch nach den anderen Besonderheiten zu urteilen, muss die *Cl. pallasi*-Rasse aus dem Weissen Meere der Untergruppe der grösseren Heringe zugerechnet werden. Ich habe nach den Merkmalen des Wachstums, wie auch nach anderen Besonderheiten mich richtend, für das Weisse Meer zwei Untergruppen der *Cl. pallasi*-Rassen festgestellt; nämlich eine Untergruppe grosser und eine Untergruppe kleiner Formen. Im Barentsmeer ist die letzte bis jetzt nicht vorgefunden worden.

Der Eingang in das Weisse Meer ist selbstverständlich eine konditionale Grenze. In geringer Zahl, den Scharen des norwegischen Herings beigemischt, kommt mitunter *Cl. pallasi* an der Murmanküste vor. Dies war der Fall bei dem von Borodatowa benutzten Material (l. c.). Im Gebiet der Insel Kolgujew, und auch an anderen Orten, lassen sich unreife *Cl. harengus* nachweisen, besonders unter denjenigen, die hierher gelangt sind, nachdem sie eine Zeit lang im Weissen Meer verweilt hatten.

Die Probleme der Herkunft und des Rassenbestandes sind sowohl theoretisch wie auch praktisch von grossem Interesse. In dieser Hinsicht ist das von mir erforschte Gebiet von besonderem Belang. Es muss zugestanden werden, dass unsere Anschauungen bezüglich der Beständigkeit der Rassenmerkmale und bezüglich der Faktoren, die Rassenbildung bedingen, noch höchst widersprechend sind; einige Forscher verhalten sich sogar höchst skeptisch gegenüber der Frage des Vorkommens von Rassen bei Heringen. Es scheint jedoch, dass die Erforschung bei solchen Fischen wie *Cl. harengus*, insbesondere in einigen Gebieten, unzweideutig auf das Vorkommen von verschiedenen Rassen hinweist. Ich werde mich darüber sehr kurz fassen. Der Rasse und ihren Merkmalen kommt eine gewisse Beständigkeit zu. Das Merkmal muss jedoch nicht allein durch gewisse Gene bedingt sein, sondern es steht auch wohl eine Wechselwirkung zwischen Genen und Umweltsbedingungen. Folglich kann ein und derselbe Genotypus, wenn er sich unter verschiedenen Umweltsbedingungen entfaltet, verschiedenartige äussere Merkmale ergeben. Die einen Merkmale sind stärker variabel, die anderen weniger. Auch vermag der Genotypus sich zu verschiedener Zeitperiode und unter verschiedenen Bedingungen zu verändern, wobei die Modifikationen, die er aufweist, besonderen Gesetzmässigkeiten unterworfen sind (parallele Reihen der genotypischen Veränderungen). Hieraus dürfte geschlossen werden, dass es Rassen mit ständigeren und solche mit mehr oder minder variablen Merkmalen gibt. Folglich muss man die Biologie der Rasse, die Bedingungen des Laichens, sowie das Gebiet, in dem letzteres zustandekommt, die Entwicklungsbedingungen

der Brut, sowie die Regionen, in denen diese Entwicklung sich abspielt, ferner die Besonderheiten der Schwankungen der Rassenmerkmale u. s. w. zu erkennen suchen. Ich will hier zwei Beispiele anführen. Ich bin, gleich S. Runnström (l. c.), der Meinung, dass die norwegischen Heringe einer einzelnen Rasse angehören; Schnakenbeck (Zeitschr. Morph. Oek. XXI, 1931) teilt sie dagegen in zwei Rassen ein. Die Differenz der Merkmale (z. B. in betreff der Vert. S.), die unter den Vertretern der norwegischen Rasse vorkommt, ist durch die Bedingungen der Verteilung der Brut entlang der Küste Norwegens zu erklären, da infolge dieser Verteilung die Brut sich unter verschiedenen Bedingungen entwickelt. Wenden wir uns nun den *Cl. pallasi* des Weissen Meeres zu. In diesem relativ wenig umfangreichen Gewässer habe ich einige Rassen vorgefunden. Die Tiefe, der Charakter des Bodens und der Küste, die Temperatur, der Salzgehalt u. s. w. sind in den grösseren Buchten des Weissen Meeres (von Kandalakscha, Onega und Dwina) höchst verschiedenartig. Die in der allerletzten Zeit ausgeführte Erforschung der Strömungen hat gezeigt, dass innerhalb eines jeden der genannten Golfe zirkuläre Strömungen bestehen. Infolgedessen macht z. B. die im Kandalakscha Golfe aus den Eiern geschlüpfte Brut daselbst ihre Entwicklung durch. Dasselbe trifft auch für die anderen Golfe zu. Auf diese Weise sind kleine oekologisch und geographisch abgesonderte Rassen entstanden[1]). Die Schwärme der ausgewachsenen Formen mögen miteinander sich vermischen, die Fische begeben sich jedoch zur Zeit des Laichens an dieselben Orte, in denen sie selbst aus dem Ei geschlüpft sind. Dies stellt nichts unmögliches vor und dürfte den allgemein bekannten Tatsachen gleichstellt werden, dass junge Kuckucke zum Winter einzeln abfliegen und dennoch den richtigen Weg unbeirrt finden, obzwar sie denselben zum ersten Mal unternehmen, oder dass junge Stare im Herbst lange vor den alten sich auf den Weg machen und richtig in die Gebiete ihrer Winterung gelangen.

Wir finden also im Norwegischen Meere an der Küste Norwegens eine *Cl. harengus*-Rasse mit Merkmalen, die in verschiedenem Masse fluktuieren, während im Weissen Meer mehrere *Cl. pallasi*-Rassen, denen der Wert beständiger Rassen zukommt, angetroffen werden (entsprechende Untersuchungen sind in den Jahren 1923, 1924, 1925, 1926, 1928 und 1929 ausgeführt worden); diesen sind beigemischt noch unreife norwegische Heringe. Aus Gesagtem ist zu ersehen, welch wichtige Rolle in der Biologie der Heringe den Meeresströmungen zukommt. In meinen Untersuchungen der Heringe des Barentsmeeres habe ich dieselben nicht allein in den Küstengebieten untersucht, sondern, da ein für Fischfang mit Treibnetzen ausgestattetes Dampfschiff mir zur Verfügung stand, diese Fische in offener See, auf verschiedener, mitunter sehr grosser Entfernung von der Küste untersucht.

[1]) Es sei darauf hingewiesen, dass, laut den noch nicht veröffentlichten Untersuchungen Kirpitschnikows, den einzelnen grösseren Golfen des Weissen Meeres besondere, besagten Golfen eigene Rassen des Stintes zukommen.

Einar Lea ist auf Grund der Ergebnisse seiner Untersuchungen zu dem Schluss gelangt, dass im Leben der norwegischen Heringe ein sogen. ozeanisches Stadium vorkommt, in welchem grosse, fette Heringe, die noch nicht gelaicht haben und unreife Gonaden besitzen oder solche, die erst im Reifen begriffen sind, sich zwei ja sogar drei Jahre lang im offenen Meer aufhalten und sich dann nach und nach den laichenden Schwärmen hinzugesellen (Ärsberetning vedk. Norges Fiskerier 1927, N IV 1928). Zur Frage, ob eine Entwicklung des Heringsfanges in offener See auf Grund des besagten ozeanischen Stadiums möglich sei, meint E. Lea, dass es für die Lösung dieser Frage gründlicher Kenntnisse bedarf über die Aufenthaltsorte solcher Heringe, ihrer Wanderungen, der Dichte ihrer Schwärme und der Tiefe, in welcher letztere sich aufhalten. Einstweilen ist darüber fast nichts bekannt.

Als ich mich anschickte, Untersuchungen am Hering in den offenen Teilen des Barentsmeeres zu unternehmen, hatte ich keine Vorgänger. Es fehlte nicht nur an jeglichen Erforschungen am dortigen Hering, sondern der Fang dieser Fische wurde dort noch nicht einmal betrieben. Ich musste also zunächst, wenn auch nur im allgemeinen, eine Kenntnis der Verteilung von *Cl. harengus* im Barentsmeer erlangen. Da ich ein ziemlich reichliches, im Laufe mehrerer Jahre gesammeltes Material über die Ernährung von *Gadus callarias* besass, so stellte ich zunächst eine Karte des Massenvorkommens von Heringen in den Kabeljaumägen auf, indem ich dazu jedesmal die Befunde der innerhalb eines der Jahre ausgeführten Untersuchungen benutzte. Das Zusammenstellen solcher für drei Jahre ausgeführten Karten brachte mir die Überzeugung, dass ich auf diesem Wege eine zwar unvollständige und von Fehlern gewiss nicht völlig freie Karte der Verteilung der Heringe ermittelt hatte. Diese Karte beruht jetzt bei der Nordischen Heringsexpedition, welche sich gegenwärtig im Polaren Institut für Fischereiwirtschaft und Ozeanographie (in Murmansk) befindet. Die Arbeiten mit Treibnetzen, die im Anschluss an die Angaben dieser Karte im Barentsmeer ausgeführt worden sind, gestatteten mir, die Richtigkeit der Ansicht E. Leas bezüglich des Bestehens eines ozeanischen Stadiums im Leben der norwegischen *Cl. harengus*-Rasse zu bestätigen. In einer 100 Meilen und darüber von der Küste entfernten Region habe ich in einer gewissen Jahreszeit grössere Schwärme fetter, unreifer, vierjähriger und älterer Heringe getroffen. Die Schwärme solcher Heringe bestehen vorwiegend aus Exemplaren gleichen Alters. Da die Unterschiede in den Körperdimensionen bei gleichaltrigen Heringen nicht bedeutend sind, so sind solche Schwärme fast gleichartig. In der warmen Zeitperiode, bei circa 11—12° Oberflächentemperatur des Wassers, hielten sich die Heringe in den oberen Schichten und dabei in so dichten Schwärmen, dass es möglich war, mit voller Rentabilität Heringsfang mit Treibnetzen zu treiben.

Das Gebiet, in dem solche Heringsschwärme auftreten, ist äusserst gross. Es lässt sich schwer sagen, wodurch ihre Verteilung bedingt ist, meine Beobachtungen sprechen jedoch dafür, dass hier der Temperatur

des Wassers eine wichtigere Rolle zukommt als der Menge der vorhandenen Nahrung (also der Menge der von den Heringen gebrauchten Organismen und nicht des Bestandes der Nahrung, des Totalplanktons).

Was die Tiefen anbetrifft, in denen der Hering sich aufhält, so stehen sie anscheinend mit der vertikalen Temperaturverteilung in Zusammenhang. Eine viel schwierigere Sache ist es, die Ursachen aufzudecken, die das Aufkommen dichter Schwärme in Buchten und Golfen bewirken, was an der Murmanküste meistens zweimal jährlich, nämlich im Spätherbst und im Winter und dann in der zweiten Hälfte des Sommers und im Frühherbst beobachtet wird. Um diese Zeit sind die Mägen der im offenen Meer getroffenen Heringe viel stärker mit Nahrung gefüllt als die der Heringe aus den Küstengebieten. Vermutlich wird also das Herantreten dieser Fische an die Küste nicht durch die Bedingungen der Ernährung bewirkt. Wahrscheinlich spielen auch hier die Temperaturbedingungen im Zusammenhang mit Salinität die führende Rolle. Meines Erachtens kommt auch eine nicht geringe Bedeutung der Mächtigkeit und dem Rhythmus des Herandrängens von wärmerem Wasser zu, das sich aus dem Norwegischen Meere in das Barentsmeer ergiesst. Dies ist jedoch einstweilen nur noch eine Vermutung. Es wäre wünschenswert, die erlangte Erfahrung summierend, in dieser Richtung Beobachtungen anzustellen nach dem Programm, das gemäss der Initiative des Conseil Permanent International pour l'Exploration de la Mer ausgearbeitet worden ist.

Die Organisation des Treibnetzfanges wurde im Sommer begonnen, in der Zeitperiode also, in welcher in der Region des Barentsmeeres die Sonne volle 24 Stunden über dem Horizonte steht. Es musste daher die Frage aufkommen, ob unter solchen Bedingungen Netzfang der Heringe möglich wäre. Es wurden Stimmen laut, die, an der Hand der Erfahrung des Kabeljaufanges mit Stellnetzen, ein Fehlgehen des Versuches voraussagten. Zahlreiche, zu verschiedenen Zeiten und in verschiedenen Gebieten ausgeführte Fänge haben jedoch höchst befriedigende Resultate ergeben. In einigen Fällen blieben die Netze nur 4 Stunden lang, bei klarem Himmel und Sonnenbeleuchtung (von 1 bis 5 Uhr nachmittags) im Wasser, und es wurden dabei durchschnittlich 100—200 kg. per Netz von 30 × 15 m. Grösse erbeutet. In Zusammenhang damit hat mich die Frage interessiert, worin die Ursache des Erbeutens fetter unreifer Heringe liegt. Meine Beobachtungen zeugen insgesamt für die Richtigkeit der von G r a h a m dargelegten Schlussfolgerungen (Journ. du Conseil, VI, 1931). Vorerst ist zu erwähnen, dass jedesmal, wenn unsere Treibnetze mit Fischen überfüllt waren, in der Nähe, wenn auch nur für kurze Zeit, Delphine *(Phocaena phocaena)* oder Schwertwale *(Orca gladiator)* beobachtet wurden. Kamen Delphine nicht vor, so wurden Heringe in den Netzen entweder gar nicht vorgefunden oder sie waren in geringer Menge vorhanden. Ein Auftreten von Kabeljau in Massen wurde während des Fanges in diesen Regionen nicht beobachtet. Mitunter fanden sich in den Maschen bei reichlichen Fängen Heringe nur an einer Seite des Netzes vor. Es kam vor,

dass die Netze fast unmittelbar, nachdem sie ins Wasser hinuntergelassen waren, direkt vollgestopft von Heringen waren. Dies geschah, wenn diese oder jene der oben erwähnten Säuger sich dicht an die Netze herandrängten. Meine Beobachtungen haben erwiesen, dass in den Regionen, die reich an fetten Heringen sind, bald Kabeljau, bald die besagten Säuger oder Weisswale *(Delphinapterus leucas)* und andere Wale sich aufhalten. Das Vorkommen von Heringen liess sich immer nach dem Vorhandensein von Seevögeln und deren Verhalten oder dem Aufkommen von Seesäugetieren erkennen. Ich habe einmal beobachten können, wie Heringe von einem Wale verfolgt wurden. Als der Wal herannahte, sprangen die Heringe in ihrem verzweifelten Bestreben, der Verfolgung zu entfliehen, mit grossem Geräusch direkt aus dem Wasser heraus. Dies bot ein ganz eigenartiges Bild.

Es ist demnach leicht verständlich, dass bei einer derartigen panischen Flucht grosse Mengen Fische auch bei klarster Beleuchtung in die Netze gelangen können. Ich habe auch Fälle beobachtet, wo in einigen Netzen Heringe buchstäblich in jeder dritten bis vierten Masche verstrickt waren, während andere in direkter Nähe befindliche Netze teilweise oder vollständig leer waren. Im Weissen Meere habe ich im Winter gesehen, wie die Weisswale die Heringe verfolgten; letztere verbargen sich bei ihrer Flucht so weit wie möglich unter dem Eis, während die Weisswale sich im offenen Wasser aufhielten. Im Barentsmeer habe ich beobachten können, wie einige Delphine einen allmählich schmaler werdenden Ring bildend, die Heringe trieben, die ihnen zu entgehen suchten und der Küste zu zogen oder vielleicht in dieser Richtung von den Delphinen getrieben wurden. Meines Erachtens findet, wenigstens in einigen Fällen, das Eindringen dichter Massen von Heringen in die Golfe seine Erklärung in dem Bestreben dieser Fische, den Verfolgungen der Raubtiere zu entgehen.

Die obenerwähnten Fälle des Fanges unreifer fetter Heringe in Treibnetzen beziehen sich auf die Versuche, die fern von der Küste angestellt worden sind. Es kommt vor, z. B. beim Eintreten der Laichperiode des Heringes im Weissen Meere, dass die Fische sich aus den Tiefen an seichte Stellen begeben und dann im Gebiete der von Algen bewachsenen Bänke der Küste entlangziehen. In solchen Fällen gelangen die Heringe bei ihrer gewöhnlichen Fortbewegung, nicht infolge der Panik, in Stellnetze und verschiedenartige andere Fanggeräte, und dann findet der Fang der Heringe in den Maschen sowohl im Wandertrieb der Fische wie auch im Massencharakter dieser Migration seine Erklärung.

Mitunter wird die Aufmerksamkeit auf Tatsachen folgender Art gelenkt. Vor zwanzig, dreissig Jahren wusste man nichts von einem Massenauftreten der Heringe in den Golfen der Murmanküste, wie es jetzt beobachtet wird. Damals wurde aber auch Heringsfang in unvergleichlich geringerem Umfang betrieben.

Ob dies an der sehr geringen Dichte der damaligen Bevölkerung der Murmanküste liegt, sowie daran, dass die Fischer ihre ganze Aufmerksamkeit dem Kabeljaufang schenkten, oder ob man annehmen

muss, dass im Laufe der letzten 15—20 Jahre die Biologie des norwegischen Herings Veränderungen erfahren hat? Ob nicht etwa ihre Laichplätze nordwärts verlagert werden? Vielleicht nimmt die Region der Verbreitung der Jungheringe an Umfang zu? Es fehlen mir jegliche Daten, die es ermöglichen würden, diese Fragen zu lösen. Heringe mit 57—58 Wirbeln kamen im Weissen Meer bereits Ende des XIX. Jahrhunderts vor, wie aus der in der klassischen Monographie Fr. Heinckes ausgeführten Analyse der Probe von Heringen des Weissen Meeres zu ersehen ist. Unbekannt bleibt aber, in welchen Mengen diese Fische dort vorkamen. Es muss jedoch vermerkt werden, dass in den letzten zwanzig Jahren im Weissen und im Barentsmeer einige Warmwasserformen aufgetreten sind, die dort früher nicht vorgefunden wurden. Ich selbst habe im Kandalakscha Golfe in den Fängen der Jahre 1924—26 Makrelen *(Scomber scombrus)* und junge *Sebastes norvegicus* angetroffen. Makrelenscharen sind an der Murmanküste angetroffen worden, sie haben Fänge von 300—400 kg. ergeben. Knipowitsch hat, des Materiales der Murmanschen Biologischen Station sich bedienend, auf eine Reihe solcher, für die Murmanküste neuer Formen hingewiesen (Bulletin de la Commission pour l'Etude du Quaternaire, N 3, 1931. Acad. d. Sc. U. S. S. R.). Ferner ist mir aus meinen eigenen älteren Beobachtungen bekannt, dass in den Jahren 1904—1906 in der Region der Bäreninsel garnicht damit zu rechnen war, mit dem Ottertrawl reichliche Fänge von Kabeljau und anderen Fischen zu bekommen, indessen ist es jetzt allgemein bekannt, wie reich an Fischen das Gebiet zwischen Spitzbergen und der Bäreninsel ist. Es scheinen also indirekte Hinweise auf die Möglichkeit einer Veränderung der Biologie des norwegischen *Cl. harengus* vorzuliegen, unbestreitbare Daten sind jedoch nicht vorhanden, es sei denn, dass den norwegischen Ichthyologen einiges darüber bekannt wäre.

On the Use of Alizarin as a Stain for the Skeletal Structures of Fishes.

By

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THE use of alizarin as a stain for such elements as fin rays, keeled scales, and vertebrae, is of high importance in the pursuit of the various racial investigations which prevail in the fishery research of to-day, and yet, to one approaching the subject for the first time, there can scarcely be said to be an abundance of guidance available. Nor is the matter wholly without its difficulties. Even by workers with no slight experience of the dye considerable diversity of results, to the writer's knowledge, is commonly encountered.

Primarily with a view to minimizing the author's own failures, some study has been given to the behaviour of alizarin as a stain. These notes thereon are put on record in the hope that they may prove of service at least to the new manipulator.

Tåning, 1927, would seem to be amongst the earliest of references as to actual staining method. While making no personal claim to the instigation of the technique he employs, he describes the staining of small fish, after preservation in neutral formalin, in a weak alcoholic solution of alizarin, to which solution a trace of dilute acetic acid has been added.

In Gatenby's edition of Bolles Lee's "Microtomists Vade-Mecum", 1928, there is included, p. 483, a method of staining the skeleton of cleared specimens with Alizarin Red S. Alden B. Dawson is quoted as stating *(in literis)* that alcoholic solutions of alizarin, as commonly used, stain soft parts as well as skeleton and must be followed by a decolorizing fluid such as an acid alcohol, or else the material must be allowed to stand in strong sunlight until the stain has been removed from the tissues surrounding the bone. Dawson, accordingly, is responsible for a method whereby fixation *in toto* is effected in 95 per cent. alcohol. Immersion for a period in a one per cent. solution of potassium hydroxide clears the tissues, after which staining in a dilute solution of alizarin in one per cent. potassium hydroxide colours only the bones. If, however, the initial clearing has not been complete enough the muscles and other tissues take the stain almost as readily as the bone itself.

Gray, 1929, gives three techniques, one regressive in aqueous

solutions, and two progressive in alcoholic solutions. The theory of alizarin staining is, according to Gray, the formation upon calcium mordanted tissues, of a lake which is insoluble in alkalis. The whole animal is therefore soaked in an alkaline solution of alizarin. Excess of stain is removed from the tissues, and the bones being mordanted with calcium by nature are left coated with a red lake. His first method, the perfection of which he states is due to H. W. Parker of the British Museum, consists of fixation in iodine alcohol, staining in a deep purple solution of alizarin in one per cent. potassium hydroxide, and differentiation, together with the clearing of the tissues, in one per cent. potassium hydroxide. The second consists of fixation in 70 per cent. alcohol and staining in a pale pink solution of alizarin in five per cent. ammonium carbonate in 70 per cent. alcohol, a certain amount of differentiation taking place during dehydration preparatory to mounting. The third, which is mentioned as specially suitable for young fish, consists of preservation in any non-acid fixative with staining in a pale pink solution of alizarin in one per cent. borax in 70 per cent. alcohol, a certain amount of differentiation again taking place during dehydration prior to mounting.

Rahimullah and Das, 1933, also contribute to the literature upon the alizarin-potassium hydroxide method of staining skeletons. Notices of their paper have appeared in "Nature", No. 3301, Vol. 131, 1933, No. 3360, Vol. 133, 1934, and No. 3386, Vol. 134, 1934. Their use of the stain is similar to that of Dawson.

Hollister, 1934, fixes fish in 70 per cent. alcohol, baths them in a one to four per cent. solution of potassium hydroxide, and stains in a weak solution of alizarin in one to four per cent. potassium hydroxide. Clearing is effected in glycerine and potassium hydroxide, ultra-violet light from an alpine sun lamp being used to speed up the process and to remove body pigmentation and excess of alizarin from the flesh.

While potassium hydroxide methods would appear to have been employed with very small fishes quite successfully both in Great Britain and in the United States, there is the objection, as voiced by Gray, that for many forms the alkali is too drastic and tends to disintegration of specimens.

Alcohol-alizarin techniques would seem to be preferable for general fishery work, for, in the first place, specimens are easily cut to reveal the vertebral column on the one side while all external features are retained intact on the other, so that there is little object in rendering the tissues of any but the most delicate material transparent, and, in the second place, there are several less drastic yet thoroughly satisfactory methods of clearing such specimens as are too small and fragile for dissection.

Of the alcohol-alizarin methods in publication there are, then, two types, that of Tåning involving the addition of acid to the staining solution, and those of Gray in which the alizarin is in alkaline alcohol solution.

Tåning remarks, however, that his method may fail or give only mediocre results, the causes of which "seem to be somewhat mysterious, but must be supposed to lie in the state of the material prior to preservation and changes taking place during storage prior to use." He also observes that very old material is often difficult to stain, adding, in parenthesis, "owing to change of acidity".

The writer's early experiences of alizarin were mainly with specimens which had been preserved for a year or more, and although every effort was made to duplicate in scrupulous detail on every occasion the different points of Tåning's technique, the results obtained varied from success to failure in all possible degrees. The use of alkaline alcohol staining solutions effected no improvements whatsoever.

Series of experiments were therefore made to test, firstly, how far acidity of specimens adversely influences staining. The hydrogen-ion concentrations of a number of solutions, in which had been preserved material to be stained, were determined by means of a B. D. H. Capillator outfit and were correlated with degree of staining success achieved.

The preserving solutions, in every instance aqueous solutions of formaldehyde, were found to vary from pH 5 in the case of very old material where the formalin, before the specimens were immersed in it, had probably not been rendered permanently non-acid according to the directions of Atkins, 1922, to pH 9 in the case of recently preserved material where the formalin of Atkins had been duly employed.

Extreme difficulty in staining was experienced with specimens from preserving fluids of pH 5 to 6, the skeletal parts remaining entirely unaffected in the bulk of such material. Speedy improvement in staining was found as the pH of the preserving solution increased to the alkaline side of neutrality, and material from solutions of pH 8 and 9 stained perfectly. Throughout these tests the specimens were taken straight from preserving solution to staining solution. The staining solution used was made up according to Tåning but without the addition either of acetic acid or of an alkali.

The next step was the staining of specimens from preserving solutions of pH 5 and 6 after washing in tap water, here pH 8.2, for periods of different duration. Washing in tap water in every instance resulted in a decrease in the pH of the washing water and a corresponding improvement in the staining obtained. The more thoroughly the specimens were washed the better was the staining achieved, although in no case was the final result quite equal to that obtainable with specimens from non-acid preserving fluids. When attempts were made to counteract the acidity of the more difficult specimens by washing in a weak alkali, subsequent staining resulted in the whole specimen, tissue as well as bone, dyeing a deep bluish-red colour.

As to the causes of acidity of preserving solutions, Atkins, 1922, pointed out that the quantities of acid found in fresh and stored

formalin are by no means negligible. He gives the pH of a carboy of 40 per cent. formalin as 2.8, and he states that a 5 per cent. solution of formaldehyde after being stored with fish for fifteen years was at pH 5.0 He also found that after rendering alkaline (pH 8.0) two litres of 30 per cent. formalin by the addition of sodium hydroxide, in 56 days, standing in the light, the pH had fallen to 5.2. Borax, however, forms a "buffer solution" possessing the property of resisting change in pH through addition or loss of acid or alkali. Atkins applied this to specimen preservation. By the addition of borax to formalin so that the solution is at pH 8.8 to 9.0, the development of free acidity is counteracted. Tåning stipulates the use of such "permanently non-acid formalin" as his preservative. Neglect to employ some sort of non-acid fixative certainly introduces one sure cause of staining failure.

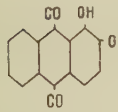
Further, fish muscle such as that of the haddock is practically neutral at death but with the formation of lactic acid as *rigor mortis* sets in, the pH, according to information supplied to the writer by Dr. George Reay, Torry Research Station, D. S. I. R., Aberdeen, falls from about 7 to about 6.4 or 6.5 steadying later at around 6.6 or 6.7. Formaldehyde, moreover, is capable of combining with the NH_2 group of the protein molecule, which, containing both carboxyl and amino groups, may react either as a base or as an acid. The combination of formaldehyde with the basic, NH_2, amino group brings into action the acidic properties of the COOH, carboxyl group. Even where permanently non-acid preservative is in use, it is accordingly a wise precaution always to use the maximum amount of preservative for the minimum amount of material, to pack preserving jars with great moderation, and to change preserving solutions with some frequency if material is in storage over a prolonged period.

Atkins, 1928, should be consulted for insight into the importance of hydrogen-ion concentration in staining in general. Watch over the pH of material to be stained is undoubtedly the keystone of successful use of alizarin.

A special series of tests was made with material which had been found to give excellent results with the ordinary non-acid, non-alkaline staining solution used in the first set of experiments. A number of specimens was stained in solutions to which acid and alkali had been added in varying amounts. Nine tubes were prepared each of which contained 25 c.cm. of dilute alizarin. To tubes 1 to 4, 2.0 c.cm., 1.5 c.cm., 1.0 c.cm. and 0.5 c.cm., respectively, of 0.025 per cent. acetic acid were added. Tube No. 5 was left untouched, and to tubes 6 to 9, 0.5 c.cm., 1.0 c.cm., 1.5 c.cm., and 2.0 c.cm. respectively, of 0.025 per cent. sodium bicarbonate were added. The nine solutions thus formed were found to approximate to pH values ranging from 7.0 tube No. 1, to 7.6 tube No. 9, the untouched tube, No. 5, corresponding to about pH 7.3 to 7.4. A range of pH of from 7 to 7.6 gives a range of colour to alizarin solutions varying from pale yellow at the one extreme to deep reddish-violet at the other. Specimens stained in these nine solutions showed no very appreciable difference, however. None

stained badly but with the more alkaline solutions the flesh was inclined to be slightly coloured, whereas, in the solutions to which acid had been added, the flesh remained in a pure white condition. The tests were repeated with batches of both good and bad material. The results in every case were the same.

Alizarin, which is dihydroxyanthraquinone, $C_{14}H_6O_2$ $(OH)_2$, with the two OH groups in the α and β positions of the same nucleus,



, is, by reason of the two phenolic groups, an acidic dye.

Professor Sir William Bayliss, 1928, remarks upon the various theories which have been advocated as to the nature of the process of dyeing, chemical or physical, in the sense of adsorption, mechanical or electrical, or in the sense of solid solution, involving partition between the solution and the tissue elements according to relative solubility of the dye therein. He expresses the view that probably all these matters play their part in varying proportion and that no one theory alone can explain all the facts. Without attempting to go deeply into the subject, however, a working explanation of the behaviour of alizarin may be built upon the principle of acidic dye and basic material.

If it be taken that an essential difference between musculature and skeleton to which the acidic dye alizarin is sensitive, producing stained bone and unstained tissue, is acidity of the tissue coupled with basic properties in the bone, then the behaviour of the stain ceases to seem in any way "mysterious". So long as the tissues are acid and the skeletal parts basic, the acidic dye will colour the basic bone and the acidic tissue will remain unaffected. If, however, the acidity of the preserving solution and of the tissues increases to such an extent that the basic properties of the skeletal parts are interfered with, the ability of the stain to colour the latter will be correspondingly diminished. If, on the other hand, the specimen is immersed in an alkali to counteract acidity, tissue as well as skeleton, becoming basic, will tend to take the stain. The limit to which the pH of tissue may fall without seriously interfering with the basic properties of the bone would seem to be around 6.5 to 7, while a preserving fluid of pH 9 is not too basic seriously to interfere with the acidic properties of the tissues.

Regarding the slightly better results obtainable with an acidified dyeing solution as compared with one to which alkali has been added, the addition of alkali to the staining bath, affecting the acidity of the tissues immersed in it, will render it less difficult for them to be coloured by the alizarin. The addition of acid to the staining solution will render it more difficult for the alizarin to colour the musculature. In great excess, of course, acid in the staining bath would interfere with the dyeing of the bone just as an acidic preserving solution does, but in the proportion used by Tåning its addition would seem to be advisable, at least in preference to an alkali.

The technique recommended is, therefore, that of Tåning, with emphasis upon the factors which have been shown to exercise controlling influence.

Material to be stained may be fixed in a five per cent. aqueous solution of commercial 40 per cent. formaldehyde. The solution must be rendered permanently non-acid, according to the directions of Atkins, by the addition of borax so that it is at about pH 9. Preserving vessels should be packed with great moderation. The preserving solution should be changed from time to time if material is in storage over a prolonged period.

On removal from preservative specimens should be washed in running water for as long a period as is practical, but at least over one night. Where vertebrae are to be counted and specimens are not too small and fragile, the flesh should now be removed from one side of the body and the vertebral column exposed. Further washing in running water is advisable. With larval forms, if shrinkage is to be minimised, the material must be passed through alcohols up to 70 per cent. strength.

A stock saturated solution of alizarin in commercial methylated spirits should be kept. Staining should be effected with a five per cent. solution of stock alizarin in 70 per cent. methylated spirits. From 0.5 to 1.0 c.cm. of one per cent. acetic acid should be added to every 500 c.cm. of staining bath. Material may be left in the stain from 12 to 24 hours according to the nature of the specimens and the depth of colour required. While staining may proceed best at about 25° C., there is no need for conditions other than ordinary room temperature. Excess of stain may be washed out in 70 per cent. alcohol. Severe overstaining may be reduced by acid alcohol.

Larval forms from which the flesh on one side has not been removed must be passed through further alcohols and cleared. Xylol, Gurr's medium or other agent may be used. In making permanent preparations of such specimens, however, it must be borne in mind, as pointed out by Atkins, 1928, p. 372, that acidity of mounting medium will result in the fading of the stain in course of time.

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On the Component of a Frequency Distribution ascribable to Regression.

By

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Introduction.

A symmetrical unimodal frequency curve is rather a rare thing in natural phenomena. Skew curves, bimodal and multimodal curves are of common occurrence. The general tendency among statisticians has been to ascribe skewness to a varying "error" applicable to the different values of a measured variate. On such grounds curves such as Pearson's Type III and the Galton-McAlister have been developed. Skewness arises also from the effect of selection. Multimodality is generally accounted for by the assumption that the population sampled is composed of two or more populations differing in their mean values.

These explanations are, of course, often true.

In the following paper it is shown that skewness and multimodality often arise by way of the manner of sampling a population. In this case the above explanations do not apply. The phenomena in question are not caused by the fact that a sample is not a *random* one, but by the fact that it *is* a sample random as to a particular dimension, which, however, has a non-random connection — a regression[1]) in fact — on the measured variate.

By random sampling as to a dimension, I mean that, as more and more samples are taken, these tend more and more to become equally spaced out in the dimension. For instance, random sampling of a variate, say length of blade of growing grass, as to area means that, in the limit, every part of the area is equally represented by measurements of blade length.

Random sampling as to time results in samples being taken, roughly at equal intervals of time, length of interval varying Normally about a mean value. For instance, in putting coal on the fires in Government offices between 11 a. m. and 12 noon, probably there is a random

[1]) In this paper I have used "regression" to mean the expression of one variate in terms of another on which it is in some way dependent.

division of time. If, therefore, sixty Civil Servants were directed to observe the room-temperature when putting coal on the fire between the stated times, the time-interval between observations would vary Normally about a mean value of one minute. The resulting frequency of temperatures would contain a component due to regression of temperature on time as an equally spaced independent variate, and another component due to variations from the regression.

The methods of this paper are applicable only in cases in which either (1) the independent variate is equally divided by the points of observation or (2) the observations are random as to the independent variate, or (3) there is a combination of the two conditions. For instance, daily temperatures may be taken "after lunch". This is an attempt at spacing out the observations by 24-hour intervals.

In this paper I have assumed, for the sake of simplicity, that condition (1) holds in all cases. This is usually the case in experimental and in observational work, where the readings of the independent variate are known. The main object of this paper is, however, to afford a means of *detecting* regressions by examination of the form of the frequency distribution of the dependent variate. In this case the independent variate will usually conform more nearly to randomness in its spacing than to exactly equal spacing. The theoretical *mean* form of the distribution will be the same in both cases, since the errors of unequal spacing will not appear in this.

The error distributions which I have dealt with in the second section of this paper do not apply to errors of unequal spacing in the independent variate[1]), but to errors or variations in the observations.

Section 1. Pure Regression Distributions.

Let us suppose that we have made a set of observations of differing values of a variate. The observations, because of the manner in which they are made, may be considered as differing also by intervals in time, by intervals in one or more dimensions of space or by intervals in some other variate. As an instance of the last case, observations of the frequency of a given letter per hundred words of an "average" book may be divided according to languages. An independent dimension, intervals in which divide our observations, I shall term the independent variate, whether its variation be continuous, or discontinuous.

The procedure adopted in Fisher's analysis of variance for eliminating variance between "blocks" of small plots of land may by considered as the fitting of a "point" regression[2]) with a discontinuous independent variate. There is a variance due to block differences of fertility, and the standard error calculated from this variance is the

[1]) See Appendix.

[2]) In a "point" regression the effect of the "independent variate" on the measured variate is either present or absent. There is no *variation* in the effect, which is either 0 or 1 when measured in the appropriate unit.

standard error of the component of the frequency distribution ascribable to point regression of crop on blocks. Here the independent variate is block fertility.

I propose here to deal only with the component distributions ascribable to regressions, of various types, in which the independent variate varies continuously. For the sake of simplicity I shall deal only with regression on a single independent variate, and shall assume that the observations differ by equal intervals on the axis of the independent variate. For the present, I shall assume also that the relation between the variables is exactly expressed by the regression; there is no variation from the regression line.

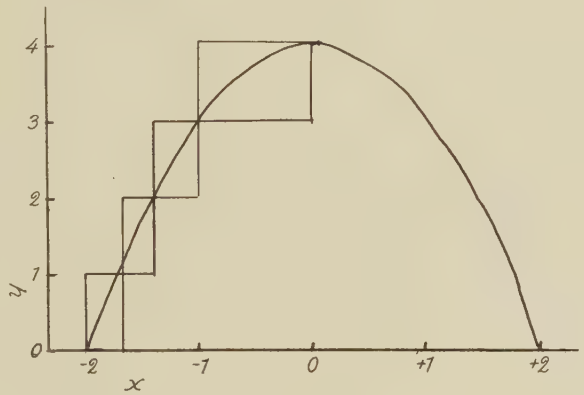

Fig. 1.

Consider now Fig. 1, which illustrates the parabolic regression of y on x. It is obvious that the number of points equidistant in the x-dimension which can be fitted on any part of the curve depends entirely on the slope of the curve. In the language of infinitesimals, the relative frequency of the observation y is inversely proportional to $\frac{dy}{dx}$. If we make y the independent variate, which will be convenient as we wish to plot values of y on a linear scale, the relative frequency of y is given by $\frac{dx}{dy}$[1]). It is plain that the relative frequency between any two limits of y is the integral of $\frac{dx}{dy}$ between these limits, namely the sum of the intersects on the x-axis by the given limits of y. It may be written thus, f denoting "the relative frequency of":—

$$f(y)_n^m = S|(x_m - x_n)|$$

Every intersect is considered as positive. If y and x, in the parabolic case, are scaled as in Fig. 1, the relative frequencies of y between $y = 1$ and $y = 0$, between $y = 2$ and $y = 1$, and so on are given thus.

[1]) See Appendix.

We have $$y = 4 - x^2$$
$$S(x) = S\sqrt{4 - y}$$
and the proportional frequencies are thus as given in Table 1.

Table 1.

$f(y)_3^4$	= 2	.500
$f(y)_2^3$	= .828	.207
$f(y)_1^2$	= .636	.159
$f(y)_0^1$	= .536	.134
$S\{f(y)\}$	= 4	1.000

It is usual to equate the total frequency to unity in cases of this sort, as in the second column.

If we take samples random as to x from a variate population of y exactly following the parabolic law illustrated in Fig. 1, the mean frequency distribution of the variate (y) will be that given. The commonest value is an extreme value, viz. the greatest. If the parabola is concave to the x-axis, the commonest value of the variate is the smallest.

An interesting regression distribution ascribable to regression of length on space is that afforded by plants, such as grass, growing in patches. We find that the longest blades are in the centres of the patches, and that the length of blade gradually decreases as we move towards the edges. The greatest decrease in length according to space traversed usually appears to take place at about that length midway between the greatest and smallest, and below this the decrease becomes slower and slower, until an even level of short grass is attained. In fact the space distribution of lengths measured along any vertical section of a regular patch appears very similar to the Curve of Error. We shall assume for the moment that the patches have this form, and are all of similar circular form in all horizontal sections. We shall also assume that the patches are close together, so that the frequency surface of lengths may be taken to extend to, say $\pm 3\sigma$ from the centres.

Samples of lengths taken at random over an area of grass will thus have a mean frequency distribution given by

$$f(y)_n^m = S|(x_m - x_n)| = S|(\sqrt{-\log y_m} - \sqrt{-\log y_n})|,$$

where x_m and x_n are points, in the area, where lengths of blade are y_m and y_n respectively. The form of the frequency distribution obtained may be deduced from Pearson's Table of the abscissae and ordinates of the Normal Curve of Error. Equal intervals in z (length

of blade) are taken, and, against these limits, the differences between the corresponding abscissae. The value of z corresponding to $\pm 3\sigma$ is .004, and the value of z at the centre of the distribution is .3989. We will therefore take ten equal intervals of plant length, each of .0395. Table 2 shows the relative frequencies:—

Table 2.

Blade Length	Abscissa	Difference	Prop. Frequency
.3989	0		
		.45	.1485
.3594	.45		
		.21	.0693
.3199	.66		
		.18	.0594
.2804	.84		
		.16	.0528
.2409	1.01		
		.16	.0528
.2014	1.17		
		.17	.0561
.1619	1.34		
		.20	.0660
.1224	1.54		
		.23	.0759
.0829	1.77		
		.34	.1122
.0434	2.11		
		.93	.3069
.0039	3.04		
		3.03	1.0000

The distribution is thus markedly bimodal, the largest mode being at the smallest plant length.

If the patches are of varying sizes and the length range of plant in the patches also varies, other modes of different heights will appear in the distribution. The large modes at the smallest size of plant will, however, coincide, resulting in a distribution that is very skew positively.

A space distribution similar to that occurring in the lengths of patchily growing plants may be expected to occur in the density of planktonic organisms, where these occur in separate patches. Each patch may be taken to have arisen from a restricted production centre. If, then, motions of the organisms are subject to unbiassed independent chances, the resulting space distribution of density in a patch may be expected to be Normal, or to have some resemblance to this form.

The frequency distribution of densities without regard to space will depend on the size and closeness of the patches. It will almost certainly have a mode at zero or near to it, and another rather smaller mode corresponding to the density of organisms in the centre of the commonest type of patch.

Turning our attention now to regression on time, we find that two of the most interesting types of regression distribution are (1) that of a variate periodic in time (2) that due to *growth*, of which the increments may be periodic.

Suppose a set of temperature observations are made over a whole year, the observations being equally spaced in time or random with regard to time. Temperature is markedly periodic, the chief period being annual. Considering this period only, we may write

$$y = \sin x,$$

where y denotes a temperature, and x_0 is the time at which the mean temperature occurs. Therefore we have, for the relative frequencies of y, between m and n, x being measured in degrees,

$$f(y)_n^m = S\,|(\sin^{-1} y)_n^m\,|$$

The following relative frequencies result (Table 3).

Table 3.

A (y)	B (Mid y)	C x (in degrees) $= \sin^{-1} y$	D $f(y)$	E $f(y)$, if $S\{f(y)\} = 1$	F $B^2 \times E$
— 1.0		90°			
	— .875		$41\frac{25}{60}$	.230	.17609
— .75		48°35′			
	— .625		$18\frac{35}{60}$	.103	.04023
— .50		30°			
	— .375		$15\frac{31}{60}$	.086	.01209
— .25		14°29′			
	— .125		$14\frac{29}{60}$	.081	.00127
0		0°			
	+ .125		$14\frac{29}{60}$	.081	.00127
+ .25		14°29′			
	+ .375		$15\frac{31}{60}$	.086	.01209
+ .50		30°			
	+ .625		$18\frac{35}{60}$	.103	.04023
+ .75		48°35′			
	+ .875		$41\frac{25}{60}$	.230	.17609
+ 1		90°			
			180°	1.000	.45936

$f(y)$ is given only for half a negative plus half a positive period, the relative frequencies being the same in the other half-periods. We see then that the simple harmonic frequency distribution is markedly bimodal, the modes occurring with maximum and minimum temperatures. Mean temperature may be a useful conception, but it is actually

the least common temperature, if temperature follows a simple harmonic law.

If there is more than one harmonic in the regression on time, the frequency distribution due to regression may take many different forms, according to the relative phases and amplitudes of the components. As an example, the curve $y = \sin x + \frac{1}{2} \sin 2x$ is shown in Fig. 2. In a case such as this where the values of the inverse function

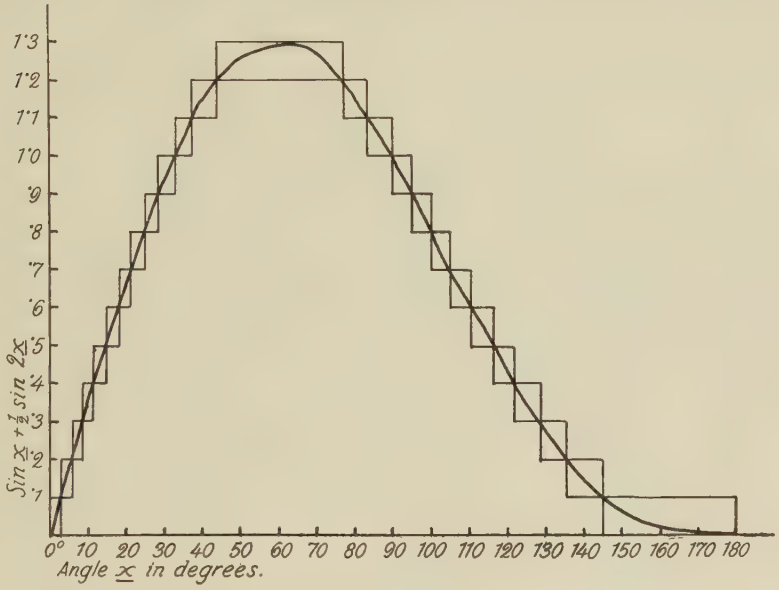

Fig 2.

cannot be computed easily, it is convenient to carry out the deduction of the frequency distribution of y graphically. In Fig. 2, y has been scaled in 13 equidistant positive intervals. The relative frequencies of the values in the intervals are obtained by summing the bases of the rectangles shown. The following are the relative frequencies obtained, approximately (Table 4).

There is thus a marked mode at the mean temperature and other modes at the maximum and minimum temperatures, the distribution being symmetrical about the mean, but having very definite, almost level "hollows" between the modes. It is impossible here to attempt to deduce the great variety of distributions arising from a composite harmonic regression. The examples given will suffice to show that multimodality does not necessarily mean that the distribution is compound in the sense of being composed of several independent distributions.

Let us consider now the second case of time regression referred to, namely that involved in the periodic growth of organisms such as plants and marine animals. The curve in Fig. 3 shows approximately a typical annual growth curve of a plaice as deduced from marking

Table 4.

y	$f(y)$
Between 0 and ± 1	37.5
„ ± 1 „ ± 2	12.5
„ ± 2 „ ± 3	10.5
„ ± 3 „ ± 4	9.5
„ ± 4 „ ± 5	9.0
„ ± 5 „ ± 6	8.5
„ ± 6 „ ± 7	8.2
„ ± 7 „ ± 8	8.5
„ ± 8 „ ± 9	9.0
„ ± 9 „ ± 10	9.8
„ ± 10 „ ± 11	11.0
„ ± 11 „ ± 12	13.0
„ ± 12 „ ± 13	33.0
	180.0

experiments. We shall assume that the curve relates to a group of 100 plaice all growing at exactly the same rate and all 10 cm. long at the beginning of January. If now we add up the frequencies of all lengths

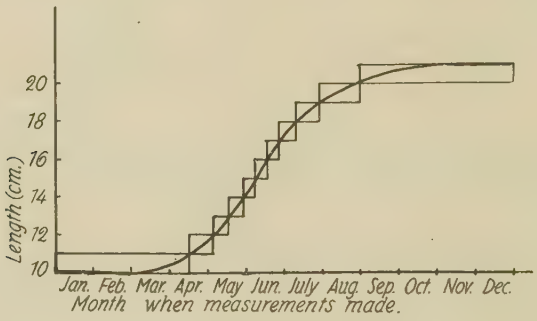

Fig. 3.

in samples taken at equal intervals of time throughout the year, the relative frequency distribution of lengths will be given by the relative lengths of the rectangles drawn in Fig. 3. This distribution is entirely due to growth — curvilinear regression of length on time — all the fish at any one time being of exactly the same length. Let us consider now the effect of "lumping together" samples over a shorter period than a year, to obtain a picture of the length distribution of fish on the ground at the middle of the period. It is easy to see that this effect is not liable to lead to seriously erroneous results, where the period is on the linear part of the growth curve, since here "lumping" samples merely increases the true spread of the distribution without disturbing its form[1]). If samples at the "curvilinear" periods are lumped together, however, the results are not true for the ground at any time, since, in effect, many more samples have been taken in the more horizontal parts of the growth curve than in the more vertical parts. The

impression given would be that of a preponderance of a *group* of abnormally small fish in spring and a *group* of abnormally large fish in autumn.

It has been said that the curve shown in Fig. 3 may be taken as a typical growth curve for plaice in some parts of the sea. It is not known, however, whether growth is continuous in the manner illustrated by Fig. 3. It is quite possible that in the growth of a plaice a check occurs in July and a "spurt" in September. Then, erroneous conclusions would be drawn from combined samples even when the period over which they are combined is a month only. It must be remembered that the relative frequency of lengths between the limits corresponding to horizontals is given by the length of these horizontals. We find perhaps that the frequency of the lengths between 23 cm. and 23.3 cm. in July and between 23.3 and 23.6 in August is the same as that of the lengths between 21.7 and 23 in June and those between 23.6 and 24.9 in September. In short, a very definite *mode* will appear at 23.30 in July and August, the distribution being much contracted compared to that in June and September. In truth, of course, there is no mode in July and August, any more than there is a "spread" in September, all the fish being of the same length at any time.

We may wish to find out what form of regression will produce a frequency distribution of a given form. This is quite a simple matter provided that the *ordinates* of the frequency distribution can be determined approximately, and expressed approximately as a mathematical function of the observations. In this case any ordinate has the mathematical form $\frac{dx}{dy}$, where x is the independent variate in the required regression and y is any observation; $\frac{dx}{dy}$ must then be integrated and the inverse function of the integral is the required regression of y on x. For example Fig. 4 shows in straight lines a simple form of skew distribution. Any ordinate is given by $f(y) = a + ky$.

Then

$$x = \int (a + ky)\, dy = ay + \frac{1}{2} ky^2 + c$$

The regression line thus has the form of a parabola, lying on its side. The observations may conform to the positive half only of this parabola. Relative frequencies are not altered by this, nor by there being a succession of these half-parabolas making contact with each other. Parts of these curves do not seem unlikely forms to be met with in nature, especially when it is remembered that the vertices of the parabolas may not be included in the observations. A very gentle parabolic slope will produce this "triangular" skewness in the resulting frequency distributions.

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[1]) This is strictly true only if the frequency distributions of lengths at each period are Normal and extend to $\pm \infty$.

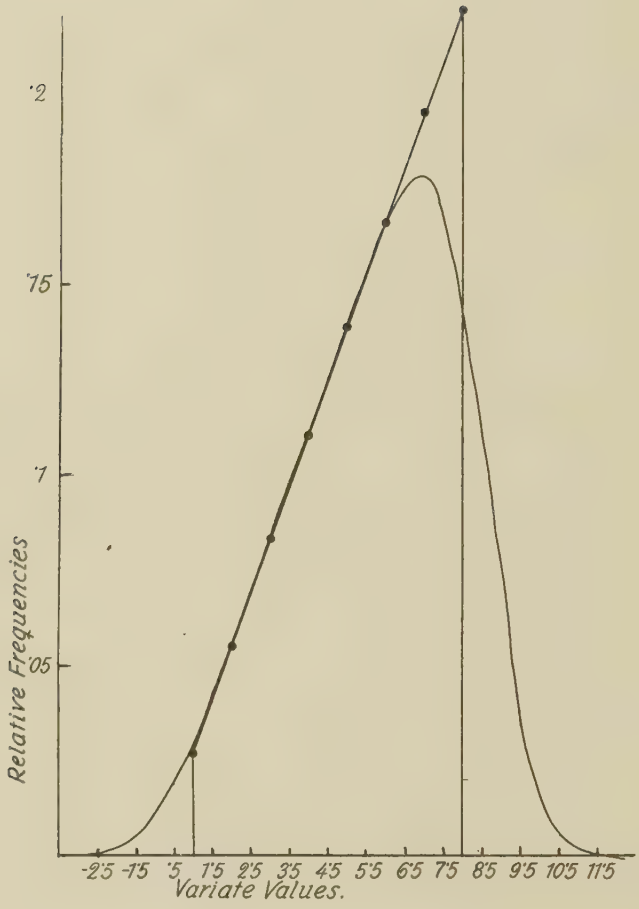

Fig. 4.

It is of interest to investigate the regression form which will produce the Normal frequency distribution. We have

$$\frac{dx}{dy} = ke^{-y^2}$$

$$x \quad k\int e^{-y^2} \cdot dy - H(y).$$

The regression line thus has the form of a Normal "ogive" lying on its side. This does not appear to be a form of regression at all likely to be met with in nature, and therefore we may feel fairly comfortable in assuming that a Normal frequency distribution indicates absence of regressions other than the linear.

Section 2.
Composite Frequency Distributions arising from Regression Components and Error Components.

The pure regression components treated in the last section can never appear in their simple form in nature, since errors or deviations from any mathematical law must be present always.

I propose now to deduce the form of some composite distributions by adding hypothetical error distributions to the pure regression forms. It will be assumed that the standard errors of all values of y are equal to one another. I shall choose for discussion at first a regression

Table 5.

(1) y	(2) $\frac{y}{\sigma}$	(3) Area[1])	(4) Diff.(A)	(5) (A×.230)	(6) (A×.103)	(7) (A×.086)	(8) (A×.081)
−1.0	−4	1.0000		(1) (8)	(2) (7)	(3) (6)	(4) (5)
−.875			.0013	.00030	.00013	.00011	.00011
− .75	−3	.9987		(2)	(3) (8)	(4) (7)	(5) (6)
−.625			.0215	.00495	.00221	.00185	.00174
− .5	−2	.9772		(3)	(4)	(5) (8)	(6) (7)
−.375			.1359	.03126	.01400	.01169	.01101
− .25	−1	.8413		(4)	(5)	(6)	(7) (8)
−.125			.3413	.07850	.03515	.02935	.02765
0	0	.5		(5)	(6)	(7)	(8)
			.3413	.07850	.03515	.02935	.02765
+ .25	+1	.8413		(6)	(7)	(8)	
			.1359	.03126	.01400	.01169	.01101
+ .5	+2	.9772		(7)	(8)		
			.0215	.00495	.00221	.00185	.00174
+ .75	+3	.9987		(8)			
			.0013	.00030	.00013	.00011	.00011
+1.0	+4	1.0000					

distribution which may be compared with distributions of actual observations, in which the approximate form of the regression is known.

I propose then to consider a harmonic regression distribution combined with error distributions. To approximate to this combination, each relative frequency from Column E of Table 3 is spread out into a Normal error distribution of the appropriate area and the results summed. The standard error of any value of y will be assumed to be $\pm .25$. The first part of the process is carried out as shown above (Table 5).

The resulting distribution is obtained as follows. Each frequency in Column E of Table 3 is considered as a Normal distribution having its mean at the centre of the corresponding y-value and having a standard deviation of .25. The relative frequencies in each cell of the compound distribution are obtained by summing Columns (5) to (8), in Table 5, diagonally, remembering that these four columns repeat

[1]) From Table 2 of Tables for Statisticians and Biometricians. Karl Pearson. Cambridge University Press, 1914.

themselves, but in reverse order, in the harmonic distribution. I have numbered the quantities to be summed for each frequency cell, the first cell, containing frequencies of variate values between — 1.875 and — 1.625, being No. 1 and so on. The resulting frequencies are thus:—

Mid-Point of Cell	± 1.75	± 1.5	± 1.25	± 1	± .75	± .5	± .25	0	Total
Relative Frequency	.00030	.00508	.03358	.09446	.12719	.10862	.08894	.08370	1

Frequency No. 9 is equal to No. 7, No. 10 to No. 6 and so on.

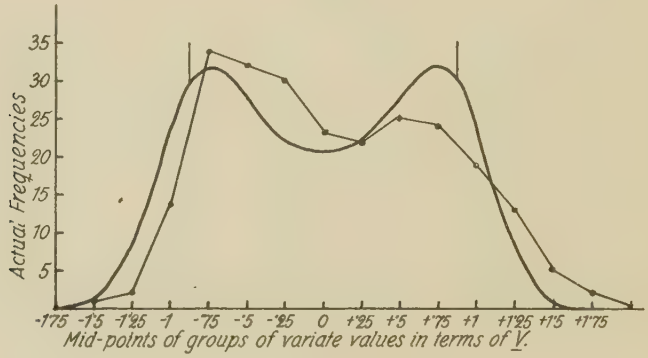

Fig. 5.

The form of the frequency distribution is shown by the continuous curve in Fig. 5. Thus a curve that appears to be composed of two overlapping curves of error may arise from a simple harmonic regression of the measured variate on time, space, or some other variable. A set of salinities or sea temperatures showing bimodality might be thought to indicate the presence of two different water masses. Yet this bimodality may be due only to *linear* change in salinity or temperature with tide, not a discontinuous, but a very simple continuous change.

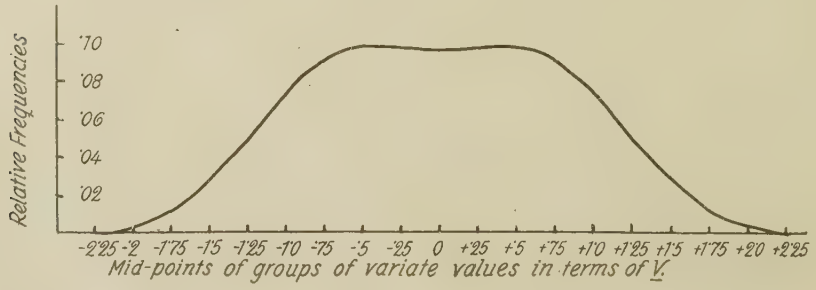

Fig. 6.

The greater the error component in a compound harmonic distribution, the more is the bimodality due to the harmonic obscured. For instance, Fig. 6, shows a harmonic distribution with standard deviation of .5 about the regression. The curve is almost an ideal flat-topped curve. Less "error" than .25 would result in a distribution having modes sharper and nearer the ends of the distribution than those shown in Fig. 5.

Let us now compare with these theoretical distributions the frequency distribution of a group of observations in which harmonic variation is known to occur. I have chosen for this purpose

Table 6.

Sea Temperatures at Seven Stones Lightvessel in the years 1903—1927.

Mid-Points	Relative Frequency of Temperatures	Mid-Points	Relative Frequency of Temperatures
7.05	0	13.35	.09175
7.75	.01310	14.05	.08801
8.45	.03183	14.75	.06741
9.15	.11047	15.45	.05243
9.85	.13482	16.15	.03558
10.55	.11235	16.85	.01311
11.25	.10673	17.55	.01124
11.95	.07677	18.25	0
12.65	.05430		1.00000

observations of sea temperature made at the Seven Stones Lightvessel in the years 1903—1927[1]). The monthly means have been used, not the original observations. It is convenient, for comparison with theory, to group the observations in about the same number of classes as is used for the theoretical distributions. The range is from 7.5° C. to 18° C., and I have divided the observations into classes differing by .7° C. The proportional frequencies are given above (Table 6).

The bimodality due to harmonic variation is clearly shown. On casual inspection there appear to be, however, a disproportionately large number of moderately low temperatures, too few moderately high temperatures and too many very high temperatures for simple harmonic variation, plus equal error throughout, to account for the observed phenomena. If we assume equally distributed error, our curve with error equal to .25 would fit the observed distribution better than would that with error of .5, whereas a distribution with less error than .25 would not account for the long "tails" in the observed distribution[2]). We shall therefore further examine the fit of the theoretical distribution with error of .25.

[1]) J. R. Lumby, "Salinity and Temperature of the English Channel, 1903—1927". In the press.

[2]) Probably a distribution with error between .25 and .5 would fit best. I am working out a scheme for finding the best-fitting distribution combining a simple harmonic and "error", for fitting to series of observations. But a general discussion such as the present paper is not the place for detail of that kind.

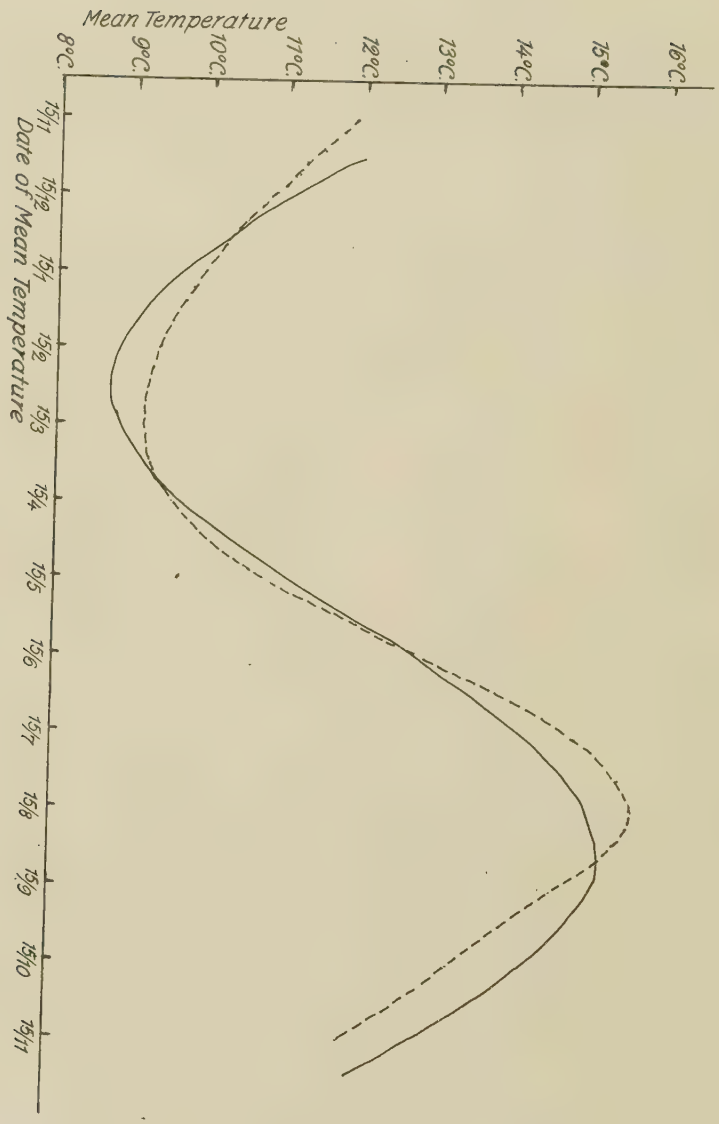

Fig. 7.

We must first of all find out what unit should be used for classifying the observations.

From Table 3, Column F, we see that the variance due to harmonic regression, with eight classes, is .45936. To this is added the variance $(.25)^2$ for error, giving a total variance of .52186, with a unit of 1. The variance of the observations is found to be 11.0927 in terms of $(.7°)^2$. This is .52186 U^2, where U is the required unit. U is thus

3.23° approximately. The mean temperature is found to be 11.9591°. The relative frequencies of observations, grouped according to the calculated unit, are indicated in Fig. 5 by dots joined by straight lines. The positions of the harmonic modes (without "error") are at $m \pm U$, i. e. at 8.73° and 15.19°, shown approximately by short vertical lines in Fig. (5). These modes are definitely outside the positions of the modes of the figure. But this is due to the error component, which has the effect of bringing the harmonic modes closer together. The error of .25 U, ascribed to the observations in the case being dealt with, may be somewhat too low, since the modes appear to be somewhat closer together than $m \pm .75\ U$.

When a regression distribution is being considered, it must be remembered that the assumption is made that nothing is known about the connection between the dependent variate — the observed values — and the independent variate. In the present instance, the time relation of the observations is assumed unknown. Nothing therefore can be said as to the phase or number of periods in the harmonic. The amplitude is the only parameter which can be estimated. Variations from the frequencies of different temperatures expected on the harmonic theory may, however, be investigated, and the results of these are useful as giving an indication of departures, from the theoretical harmonic time-curve, made by the time-curve of observations.

The departures, from the theoretical regression *cum* error curve, which have been mentioned already, indicate a distinct flattening of the time-curve in the negative part of each period, and a vertical extension of the positive part, coupled with a narrowing of the curve where it applies to moderately high temperatures. Fig. 7 shows in broken line the time-curve through the grand monthly mean temperatures, in Lumby's table referred to, and, in continuous line, the theoretical harmonic, of which we now assume that we know the phase and the number of periods. It will be seen that the indications given by the distribution are borne out in the main, but that there is a kind of bilateral asymmetry in the positive part of the observational curve, indications of which the regression distribution is not capable of giving.

The methods of this paper are not intended as a means of *fitting* harmonic or other regression lines, but as a means of *detecting* regressions which are unsuspected or have not been taken account of in making observations or in working up data. A case of the interpretation of salinity data will illustrate my meaning.

Jacobsen[1]) gives an instance of a bimodal distribution of salinities (pp. 87 and 88) from samples taken at the Lappegrund Lightvessel in the Sound, between the Kattegat and the Baltic. One

[1]) J. P. Jacobsen: "Einige Grundbegriffe und Sätze betreffs Beobachtungen, die als Wiederholungen betrachtet werden können, usw." Særtryk af Dansk Tidsskrift for Farmaci, 1930. København, 1930.

observation per day was made for a whole year. Jacobsen says "Das Auffallendste an dieser Häufigkeitsverteilung ist vielleicht die Tatsache, dass der mittlere Wert [mean value] verhältnismässig selten vorkommt". Jacobsen ascribes the bimodality of the distribution to the fact that the current (not tidal current) sometimes flows into, sometimes out of, the Baltic. He assumes thus that two different bodies of water are being sampled according to the direction of current. This may well be true. If, however, water samples were taken at equal intervals of time, not equal intervals in tidal stream, the shape of the distribution is more probably ascribable to tide, which is regression of position on time. There is very little error from the harmonic, shown by the distribution. The main discrepancy from the harmonic appears to be the preponderance of moderately low salinities. This would occur if there was a preponderant outgoing current. There is no need to assume this — "either Baltic water or Kattegat water is being sampled." The same water, gradually changing linearly with space, is being sampled most of the time, but a preponderant number of samples are being taken at or near slack water, owing to harmonic regression of position of water on time.

The use of a measure of dispersion obtained without elimination of the harmonic component is most misleading. Actually the salinity at the lightship *at any particular state of tide* might be expected to have an extraordinarily small variation. The same phenomenon may be expected to appear wherever a series of observations of salinity equally spaced in time are made, if the salinity varies gradually in space covered by the water up and down tide, and remains fairly constant at any point in that space at a given state of tide. A preponderant "error" will of course obscure the harmonic effect, and perhaps the only indication of its existence will be a greater or less degree of "flat-toppedness" in the distribution curve. Skewness such as that shown in Jacobsen's figure would probably be due either to a residual current or to the fact that the salinity of the water is not varying linearly over the tide range. The main thing to remember is that *the bimodal distribution does not necessarily indicate sampling from two water-masses having their commonest salinities at the two modes but may apply to one water-mass gradually changing in salinity with space, having no "modal" salinity, but having all salinities over a given range equally common.*

Let us reconsider now the result of combining measurements of fish made over a period of increasing or decreasing growth.

Table 7.

	cm. 10	11	12	13	14	15	16	17	18	19	20	21	22
Frequencies	0	5	15	35	50	35	15	5	0				
„	0	5	15	35	50	35	15	5	0				
„		0	5	15	35	50	35	15	5	0			
„				0	5	15	35	50	35	15	5	0	
Total	0	10	35	85	140	135	100	75	40	15	5	0	

In Table 7 are given frequencies of measurements of a hypothetical group of fish made, say, at fortnightly intervals. Between successive observations the fish are assumed to have grown, respectively, not at all, one cm. and two cm.

The resulting curve shows one large mode at about 14 cm. and has a "hump" at the right hand side, which would correspond to a group with its mode at 17 cm. In examining such a compound curve one might be tempted to interpret it as showing the immigration of a large group of small fish on to the ground, whereas only the one group has been there all the time. In the same way towards the end of the season of growth, combination of observations equally spaced in time would give a result which might be interpreted as showing the late arrival of a great number of large fish. If at any time there is a check in growth, combination of observations over the period of checked growth will give a factitious mode.

The only other combined error-regression distribution I propose to consider is the triangular distribution given by the equation

$$f(y)_n^m = S\,|\,(a + ky)\,.$$

I shall use the error distribution of eight classes given in Table 5 and shall assume that there are eight values of the independent variate, the frequencies in the regression distribution increasing proportionately to the numbers 1 to 8.

The values given in Column 4 of Table 5 have to be multiplied by the figures $\frac{1}{36}, \frac{2}{36}$, and so on, of which the total is unity. The results are written down in parallel columns and the relative frequencies in the compound distribution are obtained by summing these columns diagonally. The first frequency is thus $.0013 \times \frac{1}{36}$ the second, $.0215 \times \frac{1}{36} + .0013 \times \frac{2}{36}$ and so on. The resulting curve is shown in Fig. 4. It has rather remarkably straight sides, owing to the preponderance of the triangular regression distribution over the error distribution.

The length distribution of certain growing crops, sampled equally in space, might be expected to show a distribution similar to that just treated. The density distribution of planktonic organisms might also be expected to approximate to this, if the organisms are distributed in space in dense overlapping patches of small extent.

It should be mentioned that the forms of the compound distributions shown are approximate only, the actual theoretical frequency at any value of the variate being obtained by a double integration of the error component along the appropriate interval of the regression component. The method adopted is sufficiently accurate for obtaining types of curve for comparison with actual frequency distributions.

I think the types of regression distribution shown are those most likely to occur in nature. This is not intended to be a complete treatise, my

main object being merely to draw attention to a generally applicable means whereby it should be possible to "spot" particular causes of variation occurring in natural phenomena. The method should direct attention to these causes, and suggest lines for further investigation. I hope in subsequent papers further to develop the subject and to give detailed methods for eliminating various types of regression distributions from compound distributions. This done, the regression and variations from it become interesting subjects for study.

Appendix.

The foregoing paper has been written round the idea of a "regression distribution" because that theory affords a simple means of building up hypothetical compound distributions for comparison with observed distributions.

For actual tests of fit between theory and observations the converse method of attack, by way of $\frac{dy}{dx}$, the measure of "spread" due to regression is sometimes preferable to the use of $\frac{dx}{dy}$, the measure of relative frequency. The regression line, by the substitution of a function of y, can be changed into a straight line, but it must be remembered, if this function is substituted for the observations, that the "error" from regression is also changed and this change must be reasonable.

For instance, if the distribution of the logarithms of our observations is Normal, a reasonable explanation for this is that there is regression expressed by

$$y = e^{a + bx}$$

and that "error" from any value of y is proportional to that value. Generally, however, it is not reasonable to assume that σy_n, the "error" from any value y_n on the regression line, is the same function of y_n as is $\frac{dy_n}{dx}$, and, if this condition is not present, the substitution of a function of each observation for the observation itself will not result in a Normal distribution. The "error" from regression may be expected to be the same function of y_n as is $\frac{dy}{dx}$ only when it is caused *entirely* by random sampling error in the x-dimension.

Letters to the Editor.

Dear Sir,

In the Journal du Conseil Vol. IX No. 3 (1934) A. Bückmann in his General Article on the International Plaice Investigations during recent years writes on p. 311: "Diese Ansicht [i. e. the theory of A. C. Johansen that the plaice larvae in the Baltic do not transform into the bottom stage near the coasts, but in deeper water] erfuhr Widerspruch durch Blegvad, wurde aber neuerlich durch Kändler (26) und Poulsen (32) endgültig bestätigt". Permit me to say that this conclusion is not — to put it mildly — quite correct. Kändler and Poulsen have found a fairly large stock of the 0-group of plaice in the deeper waters east of Rügen *in the autumn* of some years, and have shown that the individuals taken in deeper water were smaller as a rule than those taken in more shallow water; but all their material comprises fish which are nearly *six months old.* The authors are therefore not entitled to conclude that the individuals which were found in deeper water *have stayed there since they reached the bottom stage;* they may quite as well originate from areas near the coasts. The fact that the individuals from the deeper water were smaller than those in shallower water may be explained by the feeding conditions being less favourable in the firstnamed places. While Kändler in August 1934 found large quantities of the 0-group plaice east of Rügen in fairly deep water ("Der Fischmarkt", H. 1. Januar 1935), I got in the same month big catches of plaice of the 0-group on the shores of Bornholm. As long as the newly transformed bottom stages have not been found in deep water in the Baltic we cannot say that Johansen's theory has been finally proved.

Yours faithfully

H. Blegvad.

Copenhagen, Feb. 8th, 1935.

IN a paper by Dr. Lissner, entitled "On Races of Herrings", which appeared in Volume IX, No. 3 of the Journal du Conseil, there appear two statements concerning the results of my herring investigations which need correction and explanation.

On page 348, Dr. Lissner states: "... it should be mentioned that Hodgson holds the opinion that the period lying between two spawning times of a herring is not always one year, but may be much

shorter or longer. Hodgson comes to this conclusion by his investigations on the breadth of the first zone in the scales of the herring."

Now, I have never held this opinion, and so far as I know, there is no evidence that herrings spawn more than once in any year. In my "Investigations into the Age, Length and Maturity of the Herring of the Southern North Sea" (Fishery Invest. Ser. II, Vol. XI, No. 7, 1929) I said, "The results of the growth calculations lead to the conclusion that autumn-spawned fish may spawn in winter, or autumn or summer in the same way that winter-spawned fish may do." This is just another way of saying that fish which are born in the autumn do not necessarily spawn in the autumn, but may spawn in the winter or spring. It does not mean that the interval between two spawning times may be greater or less than one year.

Next the author makes the following claim: "In making the assumption that the body characters of the herrings are influenced considerably by the environment we have a very simple explanation for Hodgson's observation of differences in the width of the first growth zone on the scale. For, if external influences are capable of altering the number of vertebrae and fin rays and the growth of the herrings, they should also influence the size of the scale formed during the first year of the life of the fish, which is said to be an expression of the growth of the herring."

Such a claim as this can very simply be examined and found to be a totally inadequate explanation of the differences in the modal size of the first zone of the herring scale. Let us for example consider certain herrings which are generally known as big fish such as the Norwegian spring herrings. Compared with those of the southern North Sea, these herrings are enormous, yet the size of their first growth zone is much smaller than many of the herrings of the North Sea. Again, the Baltic herrings are very small even in comparison with those of the North Sea, yet their first growth zone is much larger than the Norwegian l_1. Variations in vertebrae and growth zones do not seem to be comparable.

From my own observations, I have come to the conclusion that the factor which governs the size of this first zone on the scale is Time.

The Norwegian herrings which are born in the spring (February—March) have been found to have a calculated length l_1 of between 7.1 and 7.5 cm., and the product of the spawning at the eastern end of the Channel has been traced to herrings whose l_1 is between 7 and 8 cm. This latter spawning occurs during the months of January and February, so from the point of view of time, these two lots of fish compare very well with each other so far as the length l_1 is concerned.

Next, fish which have been traced to autumn and summer spawnings in the North Sea have been found to have calculated lengths l_1 of 9—11 cm. and 12—13 cm. respectively, and when we come to look at the small Baltic herrings we find that their l_1 varies from 10—12 cm. Now, according to Hessle the spawning time of these fish is from April until October with maxima at about June and September so we

see that a range of 10—12 cm. is comparable with the North Sea fish which are born in summer and autumn.

In my paper already quoted above, I have pointed out that the size of young herrings seems to depend more on the time at which they were hatched from the egg than on their geographical distribution, and in the cases mentioned it will be seen that the hydrographical conditions of the areas in question are very different.

In recent years much criticism has been aimed at those of us who have paid much attention to the first growth zone of the scale, and when S t o r r o w came to the conclusion that a fish which was born in the spring may not of necessity spawn at the same period, the late A. C. J o h a n s e n wrote that his argument was "a fragile basis for such a far-reaching conclusion" and then tried to explain the differences in the size of the growth zones by assuming that the herring must have either grown very quickly or very slowly as the circumstances required. Surely it is difficult to believe that a quick-growing spring-spawned herring is larger than a slow-growing autumn-spawned fish at the time that the first ring is formed on the scale, although the latter may be five or six months older than the former. But on the assumption of differential growth rate nothing is impossible.

In conclusion, I should like to add that one of the main features of growth-calculation is the rigidity of the results obtained. For many years the Norwegian fish were found to have a length l_1 which was approximately constant, and the same thing was obvious for the herrings which were spawned in the eastern part of the Channel, so that if Dr. L i s s n e r expects to find marked differences in the breadth of the first zone of the scale from year to year, the chances are that he would be disappointed.

W. C. Hodgson.

Fisheries Laboratory, Lowestoft.

Reviews.

L. H. N. Cooper. "The Determination of Phosphorus and Nitrogen in Plankton." Journ. Mar. Biol. Assoc. N. S., Vol. 19, No. 2, pp. 755—760. Plymouth, 1934.

Während Zahl, Volumen oder Gewicht des Planktons keine klare Definition seines Nährwertes gestattet, kann der Phosphor- oder Stickstoffgehalt (als Masstab des Proteingehalts) dazu dienen, verschiedene Planktonproben mit einander zu vergleichen. Da die zur Bestimmung des organisch gebundenen Phosphors bereits vorhandenen Verfahren sich nicht als zweckentsprechend erwiesen, wurde das folgende Verfahren neu ausgearbeitet:

Eine passende Planktonmenge wird mit 5—10 c.cm. Wasser in einem Erlenmeyer gespült, mit 0.2 c.cm. conc. Schwefelsäure ohne zu kochen im Luftbad eingedampft und auf etwa 160° erhitzt. Der kohlige Rückstand wird tropfenweise unter Umschütteln mit Mercks Perhydrol versetzt und schliesslich 20 Minuten lang auf 180° erwärmt. Nach dem Abkühlen wird etwa 8 c.cm. Wasser hinzugefügt und auf die Hälfte eingedampft, um Reste von Persulfat zu zerstören. Um Kieselsäure zu entfernen, wird die Lösung zentrifugiert. Nach passender Verdünnung der überstehenden Lösung wird in aliquoten Teilen die Phosphorsäure in der üblichen Weise kolorimetrisch bestimmt. Cooper findet hierbei bessere Werte, wenn er die Zinnchlorürlösung zuerst und darauf erst das Molybdat-Schwefelsäurereagenz zugibt.

Bemerkenswert ist die Konstanz des Verhältnisses des P-Gehalts zu den "Pigment-Einheiten", wie sie nach der neuen Methode von Harvey gefunden werden.

Der im Plankton gebundene Stickstoff wurde nach der von Pregl beschriebenen Methode von Parnas und Wagner bestimmt. Bei gleichzeitigen Bestimmungen des P und N im gleichen Netzfang wird 2.75 mal soviel N als P_2O_5 gefunden. Dieses Verhältnis stimmt gut mit den Zahlen überein, die Atkins früher auf indirektem Wege ermittelt hat.

H. W.

L. H. N. Cooper. "The Variation of Excess Base with Depth in the English Channel with Reference to the Seasonal Consumption of Calcium by Plankton." Journ. Mar. Biol. Assoc. N. S., Vol. 19, No. 2, pp. 747—754. Plymouth, 1934.

Schon 1931 hatte der Verfasser Anzeichen dafür gefunden, dass auch im Schelfgebiet des Englischen Kanals die "Spezif. Alkalinität" (A/Cl) sich mit der Tiefe ändert, wie es für den Atlantischen Ozean auf Grund der

Meteor-Beobachtungen kürzlich gezeigt wurde. Während im offenen Ozean diese Differenzen trotz ihrer Kleinheit mit guten analytischen Verfahren leicht quantitativ erfasst werden können, waren sie im Kanal so klein, dass Einzelwerte zur Beurteilung nicht ausreichten. Cooper wendet daher ein statistisches Verfahren auf eine möglichst grosse Zahl von Analysen an, die im Sommer 1933 nach der Methode von Wattenberg gemacht wurden. Es wird auf diese Weise einwandfrei ein vertikaler Gradient der Spezif. Alkalinität nachgewiesen. Dieser Gradient ist einer Verminderung des Kalziumkarbonatgehalts der Oberflächenschichten zuzuschreiben. Man kann ihn nicht aus einem Zuwachs des Kalkgehalts über dem Boden erklären, weil das Wasser an Kalk übersättigt ist. Der Sättigungsgrad wurde mit Hilfe von pH, t° und S $^0/_{00}$ den Tabellen von Wattenberg entnommen. Cooper berechnet schliesslich aus dem $CaCO_3$-Defizit des Oberflächenwassers die Produktion an Kalkplankton unter der Annahme dass dessen Ca-Gehalt etwa 10 $^0/_0$ betragt.

H. W.

H. Pettersson. "Scattering and extinction of light in sea-water." Göteborgs Kungl. Vetenskaps- och Vitterhets-Samhälles Handl. 5. F., Ser. B, Bd. 4, No. 4. Göteborg, 1934.

A cylindrical brass vessel was constructed with a central window and six peripheral windows. Through the central window a diverging beam from a 32 candle-power lamp was projected by a lens. The other windows received light from this beam scattered back by the sea water. This light produced an electrical current in six selenium rectifier photo cells, made by Dr. B. Lange. A robust but sensitive galvanometer was used to measure the current when the apparatus was lowered from a ship in calm water. During the day observations were made of the readings with lamp on and off, so that the scattering effect was measured by difference. Measurements of the absorption coefficient of light penetrating from above were also made. It is suggested that the preliminary results indicate a close relationship between the extinction and scattering suffered by the light, and the suspended particles of the water, notably the phytoplankton. Rapid changes, with the depth, in the concentration of the phytoplankton are found to coincide with similar changes in the optical properties and in the salinity of the sea water.

W. R. G. A.

H. Pettersson, H. Höglund and S. Landberg. "Submarine Daylight and the Photosynthesis of Phyto-Plankton." Göteborgs Kungl. Vetenskaps- och Vitterhets-Samhälles Handl. 5. F., Ser. B, Bd. 4, No. 4. Göteborg, 1934.

It was the primary object of this investigation to measure the intensity of illumination at which the rate of photosynthesis equalled the rate of respiration by phytoplankton. Flasks containing the plankton, both uncovered and covered with black cloth, were mounted on a frame with a photoelectric cell. The whole frame was lowered by sliding it along a wire running from the Bornö shore into the deep water in Gulmar Fiord, and it was thus possible to keep flasks and cell at a chosen degree of illumination by lowering and raising them in the water as the current from the cell to a galvanometer on shore waxed or waned. Since the water in the fiord was homothermal in April, the flasks were not subject to temperature changes as they were raised and lowered. The large selenium cell used was

sensitive throughout the visible spectrum and measured the light falling from above, while the flasks received a little more from scattered light coming in at the sides and from below. It seems probable that allowance, if necessary, can be made for this in due course, Dr. Pettersson being also engaged upon an investigation of the scattering of light in the sea. On the other hand, the composition of the light which has penetrated varies both with the sky conditions and with the depth and transparency of the water through which it has passed, at lesser depths there being a greater proportion having wave lengths less than 4500 A and greater than 5500 A.

During the first season's work in Gulmar fiord it was not possible to obtain phytoplankton free from zooplankton and the flasks were filled with a mixed suspension. The light intensity at which the rate of photosynthesis equalled the rate of respiration by the mixed plants and animals was found to approximate to 400 lux. As emphasised by the authors this value would have been lower if animals had been absent. They aim at continuing this investigation with phytoplankton free from zooplankton and perhaps with pure cultures of various phytoplankton organisms. The need for such investigations, under measured conditions, to fill wide gaps in our present knowledge of production of vegetation is becoming insistent, since the study of the growth of phytoplankton in the sea itself is so complicated by ever varying illumination and by the plants being continuously eaten by zooplankton.

H. W. H.

H. W. Harvey. "Measurement of Phytoplankton Population." Journ. Mar. Biol. Assoc. N. S., Vol. XIX, No. 2. Plymouth, 1934.

The aim of this investigation was to "devise a rapid method of obtaining a measure of the quantity of vegetable matter in the water . . .". The estimate of vegetable pigments (in the way first carried out by Kreps) was used as a measure of the organic vegetable matter in mixed plankton of net haul samples, caught by a net of the finest obtainable silk (200 meshes to the linear inch).

The new feature of this method is the meter which measures the amount of water which passes through the net while this is towed, lowered or raised vertically. A double release gear and throttling arrangement allows the net to be opened, and later closed at any desired depth. The meter and the release gear are described in detail and shown in instructive diagrams and photographs.

The catch was washed into the bucket and then filtered. The wet plankton was treated with 80 % acetone. After several hours the yellow-green pigment was dissolved and the colour of the solution was compared against a faintly acid potassium chromate — nickel sulphate solution. 25×10^{-6} g. potassium chromate and 430×10^{-6} g. nickel sulphate was taken to contain one arbitrary unit of pigment. The results are expressed in units of plant pigment per $m.^3$ of sea-water.

A series of vertical hauls through materially the same body of water showed that the diatoms were not distributed evenly, particularly during the summer. However, the differences do not obliterate the general picture of crop distribution which is given by this method.

From filtering a measured volume of water and counting the organisms, it was found that the unit of pigment equalled about 7,000 cells of *Rhizosolenia alata* or 224 cells of the larger diatom *Biddulphia regia*.

This method represents a great improvement as compared with the other

net methods in use. It does give the volume of the water wherein a catch of organisms has been living, though it still has the serious drawback of all net methods, viz., the loss of the nannoplankton. Variations in the composition of the phytoplankton, especially in the relative amounts of diatoms, dinoflagellates and other groups, which all have different pigmentation, may also in most places lead to unreliable results if one and the same colour solution is used throughout the year. For these reasons the method is not satisfactory as a *general* method for measuring the amount of vegetable matter in the waters, but it may be of great value for special investigations in certain waters (like the investigation of H a r v e y reviewed below). Also, it would seem to furnish interesting supplementary data when the phytoplankton production is studied by the centrifuge method and hydrographical and chemical methods now in use.

Trygve Braarud.

H. W. Harvey. "Annual Variation of Planktonic Vegetation, 1933." Journ. Mar. Biol. Assoc. N. S., Vol. XIX, No. 2. Plymouth, 1934.

The amount of plant pigment, estimated according to the method described in the paper reviewed above, was determined in the waters off Plymouth at frequent intervals throughout a year and used as a measure of the vegetable matter in the waters.

The spring diatom outburst in 1933 was described. As a whole the evidence indicated that with lengthening days and increasing sunshine the stock of diatoms increased from February to March 28th, producing daily more than was eaten by the herbivores. (The actual production was calculated from the decline in the phosphate content and from analyses of the phosphate content in diatoms, carried out by C o o p e r). The diatom maximum was recorded on March 28th, before all the dissolved phosphate was used up. A sudden outburst of larvæ at that time rapidly ate down the stock of diatoms to a low level, and kept it eaten down closely for the following five weeks, during which time the small stock was producing vegetable food for the herbivores. A rough calculation suggested that the stock was producing more than its own weight of vegetable food daily.

From May 11th to 22nd the diatom population increased and *Rhizosolenia alata* attained a density of over 30,000 cells per l. By June 12th this population had been grazed down or died down, much zooplankton and their fœcal pellets being present in the catch. On June 20th an outburst of *Rh. Stolterfothi* and *Guinardia flaccida* was found close inshore, the hauls containing very little zooplankton. It was noted that zooplankton was relatively sparse, both when *Rh. alata* was dense in May and when *Rh. Stolterfothi* was dense later, suggesting that the summer outbursts occur only when and where the demand of the herbivores slacken and, naturally, where there are enough nutrient salts.

During August lack of nutrient salts limited the production. A rough calculation suggested that, until the end of August and the dying down of the summer zooplankton, only a very small quantity of phosphate was regenerated and used again, and that the phosphorus abstracted from the water in the form of phosphate by the phytoplankton earlier in the year was kept almost entirely locked away as phosphoproteins in the animals until the end of August in this relatively shallow area. (Farther seaward it had been observed by A t k i n s that in several previous years, regeneration of phosphate took place in considerable quantity before the end of July).

In the shallow waters, which had probably some nutrient salts available, diatoms were present during August, when the water offshore was barren. In September the copepods in the catches decreased and a mixed diatom plankton appeared, and the phosphate content reached 19 mg. P_2O_5 per $m.^3$. It was suggested that rather wholesale death of herbivorous organisms and some of the carnivores dependent upon them for food was brought about at the end of August through starvation. By the end of September the plankton was sparse. During October and November there was much sunshine and few herbivorous animals in the catches; diatoms increased, maximum catches being obtained on November 22nd, when the same diatom species were dominant as in September. During the winter months of December, January and February, 1934, considerable quantities of diatoms were present. This may be an abnormal condition.

The interpretation of the observations was in accordance with the following view: "An intimate relation or balance exists between the ever-varying populations of carnivores, herbivores, and vegetable food, which in its turn is sometimes controlled and always affected by the available nutrient salts and illumination. If the proportion of carnivorous to herbivorous animals is displaced for a period by an 'abnormally' large number of carnivores, then the diatoms are free to flourish and increase their population. If, on the other hand, the balance is displaced for a period by an 'abnormally' small proportion of carnivores, then the herbivores freed from their enemies can flourish, keep the breeding stock of vegetation closely grazed and by so doing limit their own increase. This would automatically delay the utilisation of nutrient salts."

The author mentions the grazing as possibly being of special importance for the production of phytoplankton in the southern seas, where the amount of nutrient salts does not seem to set any limit for the productivity of the waters.

This investigation represents a valuable contribution to the understanding of the seasonal variation in the phytoplankton of the waters off Plymouth. The interpretation of the spring, summer and autumn maxima as caused by variations in the grazing of zooplankton seems convincingly demonstrated. Some highly interesting quantitative data are obtained on a factor of productivity for which even the roughest idea of its quantitative importance has been lacking. It is to be hoped that the author will continue his work along these lines which have proved so successful. If one should express some wishes for further publications it might be for further information on the effect of sinking, which seems to some extent to have been underrated; also for a discusssion of the hydrographical data in connection with the phytoplankton problem, and some information on the relative amount of nannoplankton and net plankton throughout the year.

Trygve Braarud.

M. V. Lebour. "Rissoid Larvae as Food of the Young Herring. The Eggs and Larvae of the Plymouth Rissoidae." Journ. Mar. Biol. Assoc. N. S., Vol. XIX, No. 2. Plymouth, 1934.

Heringslarven nähren sich bei Plymouth zur Zeit wo der Dottersack verschwindet von den Larven von *Rissoa sarsii*. Diese sind im Winter reichlich vorhanden, doch ist das erwachsene Tier im Untersuchungsgebiet nicht gefunden, vielleicht wegen Vorkommens an unzugänglichen Stellen. Es wird eine Übersicht der Rissoen von Plymouth und die Beschreibung der Eier und Larven von 9 Arten mit Abbildungen gegeben.

E. H.

M. V. Lebour. "The Eggs and Larvae of some British Turridae." Journ. Mar. Biol. Assoc. N. F., Vol. XIX, No. 2. Plymouth, 1934.

Larven aus dieser Familie sind bei Plymouth gemein und gehören zu den grössten Gastropodenlarven, sodass sie ökonomische Bedeutung haben. Es kommen 3 Arten von *Mangelia* und 6 von *Philbertia* vor. Die Unterscheidung der Larven gründet sich hauptsächlich auf der Oberflächenskulptur der Embryonalschalen. Eier und Larven der verschiedenen Arten werden teils auf Grund von Planktonmaterial, teils auf Grund von Aquarienzuchten beschrieben und abgebildet.

E. H.

F. S. Russell. "On the Occurrence of the Siphonophores *Muggiaea atlantica* Cunningham and *Muggiaea Kochi*, (Will) in the English Channel." Journ. Mar. Biol. Assoc. N. F., Vol. XIX, No. 2. Plymouth, 1934.

In den Jahren 1913 bis 1924 kam im Plankton bei Seven Stones nur die erstere Art, von 1925 bis 1934 dort und bei Plymouth nur die letztere vor. Ob *M. Kochi* auch anderwärts neuerdings vorherrschend ist, wird aus der Literatur nicht erkennbar.

E. H.

A. C. Gardiner. "Variations in the Amount of Macroplankton by Day and Night." Journ. Mar. Biol. Assoc. N. F., Vol. XIX, No. 2. Plymouth, 1934.

Die Untersuchung gründet sich auf 20 innerhalb eines Zeitraums von 48 Stunden ausgeführte schräge Netzzüge vom Boden bis zur Oberfläche, die mit einem Stramin-Ringtrawl von 5 Fuss Durchmesser in der Nähe von Liverpool in Neuschottland ausgeführt wurden. Die Euphausiden fehlten bei Tage so gut wie ganz. Auch bei *Sagitta* fielen 75 % der Individuen auf die Nachtfänge, bei *Calanus finmarchicus* und *C. hyperboreus* 61 %, während bei den Fischeiern solche Unterschiede fehlten. Die tageszeitlichen Unterschiede sind in allen 3 Fällen auf vertikale Wanderungen, nicht auf Ausweichen vor dem Netz zurückzuführen. Bei *Sagitta* verhielten sich dabei die verschiedenen Grössen nicht verschieden, bei *Calanus* gingen tags mehr Erwachsene als letzte Copepoditen (V) in die Tiefe.

E. H.

W. E. Frost. "The Occurrence and Development of *Euphausia krohnii* off the South-West Coast of Ireland." Proc. Roy. Irish Acad. Vol. XLII, Section B, No. 3. Dublin, 1934.

The normal habitat for the living and breeding of *Euphausia krohnii*, an important oceanic euphausian, is on the Atlantic Slope and to the westward. All the specimens examined came from over 100 fathoms and the species probably usually lives in even deeper waters. It always occurs in waters of high salinity and of a fairly high temperature.

Breeding apparently goes on for most of the year and a large number of larval forms has been obtained which enables the life history to be completed.

Although the larvae have been known for a long time there were many gaps in the series and Miss Frost has now succeeded in obtaining Metanauplius, 3 Furcilias and 8 Cyrtopias which she carefully describes and figures, but she has seen no eggs which could be referred definitely to

this species. There were only 3 Furcilia stages, the same number found in Mr. F. S. Russell's material from the Mediterranean (Lebour 1926) which indicates the "jumping" of some of the Furcilias. This omission of stages in deep-water forms has also been found in other euphausian larvae. A comparison with Mr. Russell's material shows that his occurred in much shallower water (only 17 fathoms depth).

It is an interesting fact that in the first Calyptopis stage only 6 terminal spines have been found in the telson, the central spine, which appears in the second Calyptopis, being absent, thus agreeing with *Nyctiphanes couchii* and *Thysanoessa raschii.*

M. V. L.

N. A. Mackintosh. "Distribution of the Macroplankton in the Atlantic Sector of the Antarctic." Discovery Rep. Vol. IX, pp. 65—160. Cambridge, 1934.

Dr. Mackintosh has analysed about 600 plankton samples taken, during the "Discovery" expeditions in the years 1927 to 1931, in the Antarctic surface waters with the 1 m. net, towed obliquely. The introduction is followed by a short description of "The physical environment of the Antarctic plankton", mainly derived from the account given by G. E. R. Deacon, (Discovery Reports, Vol. VII, 1933). The samples concerned are mostly from within the cold Antarctic surface water, only a small number having been taken to the north of the Antarctic convergence.

The conical stramin net with an opening of 1 m. diameter is fished obliquely from a depth of about 100 m. (200 m. wire) to the surface in 20 minutes. In small samples the total number of each species has been counted, but in the bigger samples this could only be done with the large species present in small numbers. The more numerous organisms were counted in sub-samples, ranging from 1/16 to 1/256 for the various species. The following sources of error are pointed out: 1) heterogeneous distribution of the organisms, 2) active avoidance of the net by larger species, 3) variations in the speed of towing, 4) accuracy of identification, and 5) "swamping" of the samples by big catches of euphausiids, salps etc.

A great number of species has been identified, viz: 3 species of Siphonophora, 2 sp. Medusae, 3 sp. Polychaeta, 1 sp. Echinodermata, 13 sp. Copepoda, 5 sp. Amphipoda, 1 sp. Mysidacea, 6 sp. Euphausiacea, 5 sp. Mollusca, 1 sp. Lunicata and the group Chaetognatha.

The various cruises are described in detail and charts given of the stations considered.

The Antarctic convergence is an important faunistic boundary, but a number of Antarctic species is reported as normally inhabiting the sub-Antarctic water to the north of the convergence.

Dr. Mackintosh has further studied the diurnal variations and their influence on the validity of the samples as indicators of the presence or absence of the different species.

Samples with the obliquely towed net are, of course, not suited for a study in detail of vertical migrations, since only the more extensive of these will be revealed by this method.

The notes and curves for the different species show, however, that some species, among them the larger copepods and euphausiids, show a diurnal variation in the samples which must be considered. For these species conclusions on their distribution and abundance are based on samples taken when they are known to be present in the upper layers.

According to the average number per haul the relative abundance of species is given in four categories: Abundant, Numerous, Moderate, and Few. (Table II. P. 97).

Calanus acutus and *Calanus propinquus* are recorded as abundant, and these species play evidently the same dominant rôle in the Antarctic plankton as *Calanus finmarchicus* and *Calanus hyperboreus* in the plankton of boreal and Arctic waters.

Euphausia superba, the southern krill, is abundant and reported to occur with an average number of 1,000 per haul, but the largest catch amounted to 190,000 specimens. The author points to the fact that this species has a tendency to shoaling. Other species seem to have a uniform distribution over large areas, many showing a preference for cold or warm waters.

Short notes are given on the distribution and abundance of all identified species, and for 10 species also the apparent distributional limits (southern or northern) are given in a chart including the areas from South Shetland to South Sandwich. (Fig. 21, p. 105). These lines of distribution run roughly parallel to the drift of the surface water and to the surface isotherms for the summer, i. e., from SW. to NE. (Fig. 22).

The distribution according to temperature is given by Dr. Mackintosh as average number per haul between the mean summer isotherms. (Table III. p. 107).

In the pages following (pp. 109 to 153) the author reports on the "Distribution of rich and poor plankton" and "Plankton communities." The text, which is of great value to all workers in marine plankton, is illustrated by many charts and synoptical tables. The more general interest of these parts is indicated in the author's summary. "The richness of the plankton varies greatly in different places and at different times. In the neighbourhood of the South Orkneys and South Shetlands, and in the eastern part of the Bellingshausen Sea the plankton appears always to be very scarce, possibly as a result of the upwelling of deep water. In other regions it is variable but generally very rich except during the winter months. It is possible that the boundary between the scarce plankton near the South Shetland Islands and the richer plankton of the Drake Passage may shift southwards in the latter part of the summer."

"Different plankton communities can be distinguished in different water masses. Fig. 48 shows roughly the different areas in which a characteristic plankton population was found. These areas coincide to a large extent with different water masses. In the outer or northern zone of the Antarctic there is a uniform plankton population which undergoes little change in composition during the year. In other places, such as to the east of the South Sandwich Islands and in parts of the Orkney-Shetland region the plankton may fluctuate sharply from place to place and from time to time. It appears that where the hydrological conditions are uniform and undisturbed there is a uniform and stable plankton, and where the hydrological conditions are complex and variable there is a variable and unstable plankton population."

In the last section Dr. Mackintosh discusses the connection between the macroplankton and the distribution of whales.

In the areas of pelagic ice-edge whaling in the Weddell Sea the plankton is extremely variable, but krill is abundant. On the old whaling grounds at South Georgia and also in the eastern part of the Bellingshausen Sea the concentration of whales in certain circumstances seems to be connected with the abundance of macroplankton. At South Shetland, in the Bransfield Strait, where whales are known to be plentiful, the plankton is normally poor.

From these findings the author draws the conclusion "that there must be more than one factor controlling the distribution of whales in the Antarctic."

In view of the nature of his material Dr. Mackintosh has drawn his conclusions with great caution, and his report is very valuable and useful as the first general account of the macroplanktonic conditions in these parts of the Antarctic.

Johan T. Ruud.

H. H. Gran. "Studies on the Biology and Chemistry of the Gulf of Maine. II. Distribution of Phytoplankton in August, 1932". Biol. Bull. Vol. LXIV, No. 2. Lancaster, Pa., 1933.

Professor Gran's study is primarily an account of eight stations made in August 1932 in the Gulf of Maine. The phytoplankton was investigated by the centrifuging of water samples. Vertical hauls of the fine plankton-net were also used for preliminary investigations. Of these eight stations, five were made in the deep basin of the Gulf and three over Georges Bank.

The same species were found in both the areas mentioned, but in the deep basin a Peridinian community was the dominant one, whereas over the Georges Bank the Diatoms occupied this position. In both areas, also, the counts suggest that photosynthesis had its maximum between twenty and thirty metres. In the Georges Bank region, though there was a slight maximum between twenty and thirty metres, the Diatoms had been distributed by vertical mixing fairly evenly throughout the water columns investigated. This mixing was especially well shown by the distribution of the littoral Diatoms. Over the deeper water on the other hand, the temperatures showed that thermal layering had taken place, and Professor Gran seems to explain the preponderance of Peridinians as due to an accumulation the result of active movement to the depths where optimal life conditions prevail. However this accumulation takes place, an examination of the catch shown in Table I and coming from station 1330 over the deep water shows that the Peridinians were absolutely more important than the Diatoms at the surface. At this station with rather warm surface water, there were 11 species of Peridinians and 14 of Diatoms. On another station, where layering was not so complete, the surface not so warm, and the nutrient salts higher, there were 25 species of Diatoms to 16 of Peridinians. A Georges Bank station, at which mixing had taken place and at which there was a still lower surface temperature, had 19 species of Diatom and only 9 Peridinians. It seems as if the Peridinians can live better than the Diatoms in warm water, poor in nutrient salts. Perhaps on account of their motility they are able to strip more food from a solution otherwise fatally low in concentration.

A second part of the paper is concerned with culture experiments to determine the effect of soluble iron compounds on the growth of certain species of Diatom. *Chaetoceras compressus, Leptocylindrus danicus, Nitzschia delicatissima, N. seriata* and *Rhizosolenia alata* all showed increased growth in sea water to which had been added nitrate and phosphate. While *Rhizosolenia alata, Chaetoceras compressus* and *Nitzschia delicatissima* showed no greater growth in solutions containing nitrate, phosphate and soil extract, or nitrate, phosphate and ferri-ligno protein, or the latter with manganese [in a second experiment with oceanic water *Leptocylindrus danicus* showed successive additional growth increments with the first and third culture solutions. *Nitzschia seriata* showed increased growth in the solution

containing nitrate, phosphate and soil extract, a less increase in the nitrate, phosphate, ferri-ligno protein and manganese] and the least, but none the less considerable one, in the nitrate and phosphate culture.

R. S. W.

H. Kuenen. "Geological Results. Pt. 2. Geology of Coral Reefs." "Snellius" Exped., Vol. 5. Utrecht, 1933.

Our author is quite frank, stating that he "spent about 40 days studying reefs and reef formations scattered all over the eastern part of the Dutch East Indies." Some 31 places were visited so that his work was of the nature of a rapid recognaissance and his charts, "simple compass and pacing surveys", show few soundings. His own observations appear to have been confined to islands and coasts and are thoroughly interesting. These entitle him to draw his conclusions as to the movements of land in respect to the sea level and as to the phenomena of the reef surface — and all careful working founded on a researcher's own observations is valuable. But our author goes further and presents a chapter "On the Formation of Atolls" which is the consideration merely of charts (to which are perhaps added the observations of others) as he himself states. I am constrained to refer to this, for my views are frequently mentioned and I cannot regard this chapter, the only one which deals with matters of importance to the question of coral reef formation, as of greater value than if written by a geologist who has never seen a coral reef. The observations made by many observers in many parts of the world are so long-continued, detailed and careful that the deductions from them cannot be skimmed in a light style. The charts here given from the East Indies are not reproduced with sufficient detail to make the topography of our author's atolls comparable with that of several well-surveyed oceanic atolls. Perhaps I am misunderstanding and our author only wishes to apply his remarks to the East Indies; and this I suspect to be the case, since I do not find any works of M u r r a y, A g a s s i z and above all D a n a even referred to. The theory of subsidence was applied by D a r w i n to *all* barrier reefs and atolls but what geologist would now claim for it such a world wide applicability? For my part while I think the foundations of many atolls have subsided, I claim that there are agencies at work to-day on coral banks that *can* transform such into atolls without movement of the earth's crust below. I do not go further and the author's *own* observations do not traverse a single one of my contentions.

Turning now to Dr. K u e n e n's article, there are recognised three small negative oceanic movements of 4—5 m., 1½—2 m. and ½—1 m., seen in three sets of levels. He is cautious but he evidently believes that these negative movements are as universal in the East Indies as I showed them to be in the Maldives in 1902. Indeed, the coral islands of these two very diverse regions seem to be remarkably similar in their coastal losses in exposed situations, in the surface structure of their reefs and in their islets washed up as banks in protected situations. In effect, it would appear that the East Indian low coral islets and their reefs are in no essentials different from those of the rest of the Indo-Pacific. Abrasion of elevated reefs on their coasts is believed to be the result of solution by the surface layers of sea water. It is pointed out that solution does not extend below low tide level, but surely on an exposed coast there is little or no surface down to 20 fathoms or so that is not covered by living organisms, through the flesh of which solution could not act. In protected situations, as in the East

Indies or as in Fiji, my observations, on which I described in 1898 the eating away of elevated reefs in many situations, cannot be due to the cutting of the waves, using carried particles, — and we cordially endorse our author's view that the matter should be experimentally investigated in the field; it may well be that the undercutting is due to solution and abrasion, both produced by organisms acting upon and in the rock, limestones being much affected as compared to volcanic rocks. The influence of larger changes of level on reef development is also discussed. There is plenty of evidence of elevation in the formation of terraces, etc., but we had hoped also to find the question of the embayed valleys of D a v i s considered as evidence for subsidence, a geological question that worries many students of reef formation.

The reef-flats vary greatly on different coral banks, but why there is a lesser dominance of dense calcareous algae on the seaward edges of the East Indian reefs is not clear. The rate of growth of corals is well known experimentally, but the rate of growth of Lithothamnioneae has not been established; it cannot be assumed to be slow. The formation of shallow rimmed pools on the reef flat is correlated with the toothed seaward edges of the reef. These latter as elsewhere are supposed to be the mode of growth of the reef seawards, while its surface pools are formed by solution. The use of the term "boulder" is puzzling, since it implies transport. Many of the "boulders" of Pelokang "grew on the spot" and retain their "original upright position"; the "boulder rampart" is the pinnacled remains of a reef slightly exposed by the lowering of water level. Similar structures, as A g a s s i z's photographs clearly show, tend to be present on most Indo-Pacific atolls; they are, as in the East Indies, "fossil formations" and their larger masses are surely what are often termed "horses". For want of a better term I called in 1898 a zone of such to seaward of the islands of Funafuti the "rough zone", employing the term "boulder zone" for an area of loose fragments torn of the reef, piled up by the seas in a line a short distance within the seaward edge of the reef-flat. At any rate the author and I agree to confine the term "negroheads" to large masses of rock, pitched on to the reef by the waves. The formation of beach sandstone is next considered, and it is deemed to be due to "evaporation of the sea water during low tide. The stratification, however, is not explained." We wish that Dr. K u e n e n had cut sections through these formations and had examined them closer, even using rock sections. I regret that I never did so, and I only know their gross morphology in a very few places. I don't agree as to the necessity of evaporation to explain cementation, believing it to be largely a surface tension phenomenon, on which view stratification is implied; possibly Dr. K u e n e n has brought home specimens on which he could test this view?

The formation of atolls is discussed, but it is considered quite apart from barrier reefs, an impossible separation in considering the theory of subsidence. The curious formation of the Toekang Besi Group is satisfactorily explained by the aid of an admirably contoured chart. The submarine slopes off East Indian atolls seem to be concave, but our author promises us a more extended report on the bathymetrical results of the expedition, and this will doubtless include slopes off many volcanic islands. Of the atolls most crown submarine ridges, and the relations of their foundations to currents, which sweep the bottom clean to below 100 fathoms, suggest subsidence as the best explanation of their formation; this quite new idea might well apply to many oceanic banks. Then follows a

consideration of interesting, submarine atoll-shaped banks, a close study of which would obviously be of great interest. As to the question of lagoon-formation Dr. Kuenen honours me. Where is his evidence that "the solvent action is limited between the tidal range" — the action of the sea "sawing" into limestone is not solution — and that "a gradual filling up appears to be the general rule for lagoons". It is not in his text, nor can I find on what he bases this statement; it is quite opposed to Darwin's view. He further remarks that "it is surprising that this results in horizontal lagoon bottoms", while I contend that such floors are impossible in lagoons that are filling up as suggested. I considered solution "to be largely a biological phenomenon due both to organic decay and to the chemical action of the ever present boring organisms". In effect, Dr. Kuenen's views on the purely physical side are not accompanied by evidence upsetting the conclusion which my collected evidence impelled me to reach that "the building and shaping of (oceanic) atolls can be explained on the basis of the chemical, physical and biological forces, both constructive and destructive, still in action in these oceans" *(Coral Reefs and Atolls,* p. 142. 1931). We hope that fate will send Dr. Kuenen again to the East Indies to make an intensive examination of coral reefs; I feel confident that such a visit would be a great scientific success.

J. Stanley Gardiner.

S. V. Segerstråle. "Studien über die Bodentierwelt in südfinnländischen Küstengewässern." Soc. Sci. Fennica, Comm. Biol. IV, 8 und 9. Helsingfors, 1933.

In 1911 C. G. Joh. Petersen and S. Ekman published their well-known papers on new instruments for quantitative investigation of the bottom fauna in Danish waters and in Swedish fresh waters, since when an important literature has appeared on results of investigations undertaken by means of these quantitative bottom samplers. In particular, Alm, Naumann and Lundbeck have used them for freshwater investigations; as regards the sea Davis has worked in the western North Sea, Stephen in the northern North Sea, Ford in the English Channel region, Hagmeier in the southern North Sea, Thulin and Hessle in the southern Baltic, Spärck at Iceland and the Faroes, Zenkewitch in the White Sea and Thorson off the eastern coast of Greenland.

The work under review is the first report on quantitative investigations of the bottom fauna made by means of the bottom sampler in *Finnish* waters; it appears as an introduction to a series of coming reports and consists of two parts, the first of which describes the area of investigation, technique, and material, while the second part gives a survey of the animal life of the sea bottom, with special reference to production.

The major part of the investigations made during the years 1922—23 and 1926—32 relates to the neighbourhood of the zoological station at *Tvärminne,* at the south-western extremity of Finland; the rest were made near *Pellinge,* in the middle of the south coast. The object was to survey the conditions of production on the sea bottom, and to study the ecology and biology of the more important bottom-living animals.

The greatest depth in the area investigated is 41 m. The nature of the bottom varies between hard sand and soft organic detritus ("Gyttja", "Mudd"). The mean temperature of the sea during the years 1927—32 varied at one station in the Tvärminne district (depth 3 m.) between 6.2° and 8.1° C., and at another (30 m.) between 3.0° and 4.9°. The maximum

temperature was recorded by the end of July at the former station, while at the latter it occurred about the middle of September, i. e., about six weeks later. The salinity of the bottom water varied during 1927—1932 between 0.21 ‰ and 7.41 ‰, the mean salinity at 30 m. depth being 6.14 ‰; oxygen varied between 5.48 and 9.45 cm.³/l., the H-ion concentration between pH 7.4 and 8.3.

The quantitative bottom samples were taken with bottom samplers of the Ekman-Birge type covering an area of 225 cm.² (Pellinge) and 234 cm.² (Tvärminne); some additional samples were secured by dredge. The author mentions various disadvantages of the bottom sampler used by him, such as the weight not being heavy enough and a tendency to close too early at the deep stations. One feels inclined to ask why, for these open sea investigations, the author has used an instrument constructed for use on soft bottom deposits in fresh waters, and not the Petersen bottom sampler which is constructed especially for use in the open sea, and which is heavier as well as bigger than the Ekman instrument.

During the years 1922—23 and 1926—32 the author took 3,273 bottom samples, a number which — owing to the small surface of the bottom sampler used — only corresponds, however, to a total surface of 76 m.² investigated. In addition 75 samples were taken with the dredge. The author's object was not only to survey the quantitative composition of animal life, but also to investigate variations with season and from year to year, and for this purpose certain stations were investigated regularly.

In the second part of the report the several more important kinds of fauna have been considered according to distribution and to conditions of production. From the report and from the extensive tables of quantitative samples, in which both number and weight of each species are given, it will be seen that the most common species are the following: *Macoma baltica, Pontoporeia affinis, Corophium volutator, Gammarus locusta, Chironomidæ, Mesidotea entomon, Halicryptus spinulosus, Harmothoë sarsi, Cardium edule, Mytilus edulis.* Of these *Pontoporeia, Halicryptus* and *Harmothoë* appear exclusively or mainly at the greater depths; *Mesidotea* may occur at all depths, while the rest of the species above mentioned occur mainly or exclusively in comparatively shallow waters. Thus the animal life becomes more uniform in appearance with increasing depth. At Tvärminne, for instance, 26, 16 and 14 species were represented at depths between 1—10, 11—21 and 22—41 m. respectively.

The number of individuals within a single species varies between 3 and 7,006 individuals per square metre. The crustaceans, *Pontoporeia affinis* and *Corophium volutator,* were taken in greatest numbers but *Macoma baltica* and *Cardium edule* were also numerous, with 1,795 and 3,000 individuals respectively per square metre. Next come the Chironomids (especially *Chironomus plumosus)* with 1,662 individuals per square metre.

Considerable *variation* in number and weight *from year to year* is recognised for several of the species; thus, for *Pontoporeia,* maxima are more than 30 times as great as minima on certain stations. The greatest quantity of the Chironomid larvae found was 5 times the lowest. As regards *Macoma baltica* the author points out the interesting fact that at the greatest depth there may be almost no annual supply of larvae to the stock for several successive years, up to at least ten years.

Variation in the number of animals *with season* is also shown; thus *Chironomus plumosus* larvae showed a distinct minimum in mid-summer and early autumn, due to the metamorphosis of the larvae. With *Corophium,* maxima were found in the autumn, as this species breeds during the summer.

The *total weight* of all animals per square metre varied between 25 and 206 gm. per square metre on "Gyttja" bottom; the *total number* varied between 111 and 7,604 individuals per square metre. In respect of number as well as weight the Tvärminne district showed higher figures than the Pellinge; it should be mentioned, however, that the samples were taken in different years and are therefore not strictly comparable.

Comparing the *total numbers* per square metre at various depths of "Gyttja" bottom it will be seen that they decrease from shallow water down to 19—28 m. and then increase in the deeper zone, 31—37 m. This is due to the fact that the more common species, *Chironomid* larvae and *Corophium*, become rarer from shallow towards deep water. The increase in number towards deep water is due to a single species, *Pontoporeia affinis*. On the other hand, the *total weight* steadily decreases from shallow water towards the deep, due to a decrease in number of *Macoma baltica*, *Chironomids* and *Cardium edule*.

Only a few species predominate in both number and weight in the "Gyttja" bottom areas; in shallow water *Macoma baltica*, *Pontoporeia affinis*, *Corophium* and *Chironomids* predominate in number; the deeper water is characterized by two species only, *Macoma* and *Pontoporeia*. This fact is still more pronounced if weight only is considered, all other species being of practically no importance as compared to *Macoma baltica*. So heavily does this species predominate in weight that in shallow water its weight amounts to 70—100 % of the total weight of all animals. At 10—30 m. depth it amounts to 90—100 % of the total weight, and in still deeper water the percentage varies from 70 to 90 %, *Pontoporeia* participating here with 13—26 % of the total weight.

Great quantities of *Pontoporeia* were caught on "Gyttja" bottoms with loose red algae *(Phyllophora, Furcellaria)*, but other crustacea such as *Gammarus* and *Mesidotea* were also more numerous here than on the naked soft bottoms.

It is clear that this work gives a great deal of particularly useful information on the character and composition of the bottom fauna in these Finnish waters. The somewhat lengthy report also contains a number of tables, diagrams and figures (showing, amongst other things, the bottom animals in their natural size and density per square metre) including aerial photographs of the districts investigated. Although the *plates* are beautifully represented, the charts and diagrams are on much too small a scale (especially those opposite page 62) and the use of them is, therefore, somewhat limited.

Considering the great number of samples taken and the amount of work evidently carried out one might have expected more extensive information on the biology of the species, their growth, spawning season, age, annual production etc., but probably the author intends to consider these problems more closely in the contemplated continuation of this work, to which the present work may be considered a good introduction.

H. Blegvad.

E. C. Scofield. "Early Life History of the California Sardine *(Sardina caerulea)*, with special reference to distribution of eggs and larvae." Div. Fish and Game, Calif., Fish. Bull. No. 41. Sacramento, 1934.

Ce fascicule donne les résultats obtenus au cours de quatre années de recherches (1929—1932) entreprises dans le but de pouvoir déterminer à l'avance l'importance de chaque classe dans la composition du stock des

sardines pêchées sur les côtes de Californie. Pour cela on a d'abord cherché à délimiter l'emplacement des aires de pontes, à s'assurer que la situation de celles-ci variait peu d'une année à l'autre, à faire une étude quantitative des oeufs et des larves, à suivre ces dernières dans leurs migrations et leur croissance. Au cours de ces quatre années, 358 stations ont été effectuées couvrant une surface de 25,200 milles carrés.

Il a été reconnu que, si l'aire totale de ponte s'étend sur une largeur de 250 milles du Cap San Lucas au N. de San Francisco, l'aire principale de ponte est beaucoup plus réduite; large de 200 milles, longue de 100 milles, elle s'est trouvée chaque année localisée dans l'espace compris entre San Diego et Point Conception. Dans cette région, les captures accusent deux fois plus d'oeufs et de larves que dans toute l'étendue de l'aire de ponte. Une pareille concentration des reproducteurs sur une aussi faible étendue est tout-à-fait remarquable. Cela tient en grande partie aux conditions requises pour la ponte qui ne peut s'effectuer dans des eaux dont la température est inférieure à 15° C. L'importance de ce facteur se traduit d'ailleurs par les quelques fluctuations observées d'une année à l'autre dans la délimitation précise de l'aire principale de ponte qui s'étend plus au moins vers le large suivant que la température est plus (1930 et 1931) ou moins (1929 et 1932) élevée.

D'une ponte abondante, on ne peut déduire une bonne année de pêche qu'à la condition de suivre le sort des larves. C'est pourquoi on s'est employé à rechercher leur lieu de rassemblement. Le jeu des courants fait qu'elles sont entraînées vers le S. de Point Conception jusqu'au voisinage de Magdalena Bay. On peut en faire dans ces parages d'abondantes récoltes en pêchant à 15 brasses environ de profondeur, et suivre leurs transformations jusqu'à la taille de 35 mm., c'est-à-dire jusqu'à leur métamorphose.

Dans les jeunes stades, elles se nourrissent presque exclusivement de Copépodes, tandis que les Diatomées font la base de la nourriture des immatures et des adultes. Cela tient à ce que le filtre branchial n'est définitivement constitué et n'est apte à retenir les proies de faibles dimensions que lorsque l'alevin a dépassé 100 mm. de longueur. L'auteur suit avec soin ces modifications importantes et donne une description détaillée de l'oeuf et des stades larvaires et post-larvaires.

L. F.

C. F. Hickling. "The Natural History of the Hake, Pt. IV. Age-Determination and the Growth-Rate." Min. Agric. and Fish., Fish. Invest., Ser. II, Vol. XIII, No. 2, 1933. London, 1933.

In this, the fourth of his serial papers on the natural history of the Hake, Mr. Hickling sets out the conclusions he has reached on the difficult questions of age and growth-rate. The difficulty lies in the fact that in this species none of the methods usually available, otoliths, scales or length frequencies, is entirely satisfactory. Scale reading after a trial was rejected as unreliable. Of the otoliths only about 40 % could be read with confidence and a further 40 % read at all. The length frequency curves, drawn from the market measurements and from the catches of the research vessel, showed a series of modes which advanced in length from month to month and agreed fairly well in position with the sizes in successive years deduced from the otolith readings.

Using the last two methods of estimation the author deduces for the hake an average increase in length of a little under 9 cm. per annum for the first eight years of its life. The hake, unlike, for example, the plaice

and the herring, increases by approximately equal length increments for about eight years, after which its growth appears to slacken, the falling off being much more marked in the male than in the female, due in the author's opinion to the increasing strain of the development of the male gonad. The annual growth is shown to be seasonal, occurring mainly from April to July.

The almost complete absence from the trawls of one-year-old fish is believed to be due to a longer pelagic life than was previously suspected. The fish first appear in any considerable numbers, even in the sprat-mesh covers to the trawl, at an age of two years and a size of 18—20 cm.

Mr. Hickling makes no secret of the difficulties he has had with his material. For instance, from time to time many of the otoliths gave readings which did not tally with the groupings of the frequency curves and which could only be explained as misreadings. Again, on the voyage of the research vessel in 1930 small hake were consistently very scarce, contrary to expectations and to the results of other cruises. It is surmised that the net may have been fishing abnormally, though no other evidence of this can be adduced. In spite of such discrepancies, however, there seems to be an ample basis of indisputable facts to support the author's conclusions, nearly 26,000 otoliths having been examined and 54,000 fish measured from the cruises of the research vessel in addition to the market measurements.

Attention may be called to one observation, namely, that the measurements of the two-year-old fish, covering a range of 12 to 30 cm., do not in any one sample form a single frequency curve but tend to fall into groups, the modes of which are approximately similar in position, though not in magnitude, from sample to sample and from year to year. These groups, the author suggests, represent the offspring of the lunar spawning periods. If this hypothesis should prove to be valid it will be remarkable evidence of the uniformity of conditions of growth, not only over the whole area, but from year to year.

The consideration of the practical application of his conclusions, namely the forecasting of the future yields of the fishery, is postponed by the author to a future paper, but one point of considerable economic importance is referred to with reference to the avoidable destruction of unmarketable fish. It is calculated that the use of an 8 cm. mesh, in general use by steam trawlers when the paper was written, involved the rejection at sea, by Milford trawlers alone, of about 2½ millions of unsaleable small hake in a year. The substitution of a 10 cm. mesh, though not doing away completely with this rejection, would reduce it by about 60 %, a saving of about 1½ million fish from this one port.

G. P. F.

R. A. McKenzie. "Cod Movements on the Canadian Atlantic Coast." Contrib. Canad. Biol. and Fish. Vol. VIII, No. 31. Toronto, 1934.

From 1925 to 1933 nearly nine thousand cod were marked by Canadian workers on the Atlantic Coast, and 727 cod were recaptured. Mr. McKenzie analyses the returns from four localities, in which he finds sufficient data.

In describing the data he divides the cod according to their movement. Thus a proportion of the stock in localities where the conditions were suitable throughout the year appeared not to move more than 20 km. and these are said to show "restricted migration". In other cases there may be orderly "extended migration" (as in the familiar case between Lofoten and Finmark) and other fish are shown to be "rovers", that is, exceptional fish

showing no apparent order in their movements. The rovers in these experiments were no larger fish than the other cod.

These categories undoubtedly help in the analysis of the material and, furthermore, the author believes with good reason that the sedentary and migratory cod are distinct stocks. Thus at Shelburne in Nova Scotia in 1926 cod marked in June and August yielded practically all recaptures within the locality of marking, whereas 20 and 25 % of recaptures of cod marked in July and September came from further away. The deduction is that in July and September a visiting school was encountered.

The analysis of returns by month and depth is carried through so as to result in definite conclusions as to movements of the cod. The author and those who carried out the marking are to be congratulated on the substantial addition made to knowledge of these fish. We are not, however, told much about the length of the fish, and nothing at all about maturity and spawning. From such length data as are given the results would seem to apply mainly to immature fish, although some of those which had been at liberty for four years must have been mature. More information on this point would have been welcome. *M. G.*

F. N. Clark. "Maturity of the California Sardine *(Sardina caerulea)*, Determined by Ova Diameter Measurements." Div. Fish and Game Calif., Fish Bull. No. 42. Sacramento, 1934.

The California sardine is rarely caught in the ripe condition, only 39 mature or nearly mature female individuals occurring in investigations extending over 12 seasons. The inconsistency of general assessments of degree of maturity by eye proving an additional difficulty, series of measurements of ovarian ova had to be undertaken to obtain information relating to the reproduction of the species. Material was collected all the year round for five years and from four locations. Samples of the eggs of 3,000 females were measured.

Four groups of ova were distinguished by the author in the ovaries of the nearly ripe specimens captured. The first consisted of eggs invisible to the naked eye, up to 0.2 mm. diameter, and was also encountered in ovaries throughout the entire year. The second consisted of opaque eggs, 0.3 to 0.5 mm. diameter, which also occurred in most adults from late December to July or August. The third consisted of opaque eggs 0.5 to 0.7 mm. diameter, and also occurred in many adults from late January to July or August. The fourth consisted of transparent ova almost ready for spawning, 0.9 to 1.23 mm. diameter, and was met with only in the 39 nearly mature females taken. The ova of the first group greatly outnumbered those of groups two, three, and four.

Following detailed analyses of the numbers of groups and their modal sizes in different ovaries, of the rates of growth of the various groups of maturing ova, and of the decrease in the ratio of number of maturing to number of mature eggs as the season advances, the conclusion was arrived at that individual sardines spawn more than once in a breeding period, ripening on the average three batches of ova per year.

The numbers of eggs in the largest group in eight ovaries were estimated, the method consisting of counting the number in a sample of known proportion by weight. The numbers increased with length of fish, varying, in a range of from about 19 to 27 cm., from 30,000 to 65,000 eggs. On a basis of three spawnings per season, the total productivity at such sizes would therefore be between 90 and 200 thousand eggs.

Size at first maturity was determined by classing as ripening to spawn in the season of their capture all fish in which ova other than of the microscopic group were found. In the shoals of the commercial fisheries no spawners of less than 16 cm. occurred, about 50 % at sizes of 18 and 19 cm. were ripening, about 90 % at 20 cm., and all of 21 cm. and over. It was also found that larger fish mature the earlier in a season, spawn over a longer period, and produce more batches of ova than smaller specimens.

Amongst other matters elucidated by the investigation was the extent of the spawning period, which was found to be from February to August, the peak months being April and May. The amount of spawning in different localities was ascertained and correlated with water temperature and shoal movements. The maturing of the sexual organs was also seen to cause a loss in body-weight during spring and summer months, the larger the fish the greater being the loss in proportion.

This careful and extensive paper, the fifth of a series upon the California sardine by the same author, is of special interest in view of recent research upon ovarian development, maturity, and fertility, in various European species, by Hickling, the reviewer, and others, with the principles of which it is in broad agreement. The possibilities of egg diameter investigations on similar lines in difficult species in general would seem to be worthy of wide attention.

D. S. R.

E. M. Poulsen. "Biology of the Dab in Danish waters." Rep. Danish Biol. Stat., XXXVIII, 1933. Copenhagen, 1933.

The increased importance of the dab to the fisheries, especially inside the Skaw, has aroused greater interest in the biology of this species. A valuable contribution to the knowledge of this subject has been given by Dr. Poulsen's work on the dab in Danish waters.

In the introduction, the author discusses the considerably increased yield of the Danish catches of dab in the 5-year period 1926—1931 as compared with the period 1909—14. In the Kattegat the yield has increased tenfold, in the Belt Sea it is 5 times and in the Baltic proper it is about 40 times as big as in the latter period. The catch of dab amounted in 1931 to 2.08 % of the total value of the Danish fishery, as against 0.18 % only in 1910. The mean value of the catch increased from about 40,000 Kr. per annum in 1909—14 to nearly $^3/_4$ million Kr. in 1930—31. The most important areas for dab are the Kattegat, the Belt Sea and the southern Baltic.

In the North Sea and the Skagerak the dab appears mainly within the 20 m. line; in the Kattegat it is most numerous within the 40 m. line, while in the Baltic it generally lives at a depth of 60 to 80 m. The cause of this divergency in the distribution in the Baltic the author considers to be the lower salinity. The difference in the occurrence of the young plaice and the dab is seen in the fact that the younger year-classes of the dab (the 0 and I-groups) keep to the 10—20 m. depth, while those of the plaice live in the more shallow coastal regions. An emigration towards deeper water with increased age is, however, also observed in the case of the dab.

Dr. Poulsen briefly touches upon the question of possible race variations between the dab from the Baltic and that from the North Sea, and demonstrates the existence of a lower number of anal fin rays in the Baltic dab and a somewhat lower number of vertebrae, and also the fusion of adjacent vertebrae occurs more frequently. He also discusses the

spawning season of the dab and shows that this is generally rather long; he gives the following spawning seasons: for the North Sea, January to June—July: for the Kattegat and Belt Sea, February to June: and for the Baltic, April to August.

A very instructive part of the report is that on the growth of the dab. From this it appears that in the transition between the 0 and the I-group the dab has an average size in the Baltic of about 3 cm., in the Belt Sea about 4 cm. and in the Kattegat and North Sea over 4 to 5 cm. The growth of the dab of higher age is also somewhat different within the various areas, and especially noticeable is the slow growth in the Baltic. The details given by the author seem also to show that variations in growth increment may appear within relatively similar districts, such as the North Sea, a fact which the author attributes to higher or lower density of the stock. As regards the low growth increment in the Baltic he also agrees with Hessle in attributing this to the over-population and poor feeding conditions. Dr. Poulsen emphazises facts previously stated by Molander that the growth in the Baltic increases with the increase of the fishery during later years. He also observes, in common with other authors, that the females have a considerably quicker growth than the males. In this connection some of the figures given by the author on the mean size of the dab at maturity should be given: in the North Sea ♂ 16, ♀ 22 cm.; in the Kattegat ♂ 12, ♀ 16 cm.; in the Belt Sea ♂ 9, ♀ 14 cm.; and in the Baltic proper ♂ 8, ♀ 17 cm. The values for the mean length of the females from the Baltic may be considered less reliable than the others, owing to the comparatively fewer data. Generally speaking, females ripen at a greater length than the males. From a biological point of view the above-mentioned figures are of great importance, inasmuch as they show that no consideration need be given to the protection of spawning dabs when fixing a minimum size. When the dab begin to spawn they are too small to be of any economic value to the fishery.

Finally the author gives details of the dab in the Limfjord. This dab migrates as a 1-year old fish from the North Sea through the Thyborön Kanal during spring and early summer. When ripe they return to the North Sea, and thus the stock of the Limfjord consists of young fish only.

The publication under review may be said to provide important information when possible measures for the protection of the dab within these waters are to be considered. *Molander.*

J. Le Gall et E.-P. Priol. "Observations sur la Ponte de la Sardine du Nord du Golfe de Gascogne et de la Manche." Rev. Trav. Office des Pêches Marit: Tome VI, Fasc. 3. Paris, 1933.

In this paper the authors report their having located a sardine spawning ground — hitherto unrecorded — off the west coast of Brittany. That spawning must be taking place on this ground was suspected when, towards the end of May and the beginning of June, 1932, it was noticed that large and obviously sexually mature sardines were being landed at various Breton fishing ports from areas situated 20 to 25 miles south-west of Penmarch, 15 to 25 miles west of Ar-Men, and 15 to 45 miles west to north-west of Ushant. This assumption was verified shortly afterwards during a visit to the Ushant grounds. There fully mature sardines were found to be plentiful and sardine eggs at different stages of development were numerous in the plankton. In the course of a trip to the same ground during the same season in 1933 these findings were repeated.

Evidence is also put forward which suggests that in these shoals of spawning fish there is a definite segregation of the sexes, the females swimming much nearer to the surface than the males. In the bottoms of mackerel nets shot on these grounds considerable numbers of sardines are frequently caught — almost all of them females. In the sardine nets, however, which are suspended at greater depths, females and males are taken in equal numbers, but the former are found enmeshed in the upper parts of the nets and the latter down below.

G. A. S.

Collection ("Sbornik") of papers on fishery work on the Murman coast. Ed. by S. J. Mittelmann (Central Sc. Fishery Institute) Moscow and Leningrad 1932. (In Russian, some with German summaries).

This collection, forming a volume of 200 pages of the modest appearance now usual in Russian publications, contains 12 short papers on several northern fishery questions, mostly pertaining to the biology of cod and haddock. — One of the papers, however, is a translation of an English paper on the whiting by H. O. Bull.

These papers are based on work done at the fishery research station at Portshnikh on the Murman coast, during the years 1927 to 1930, including *inter alia,* two expeditions sent out to investigate the fishery possibilities on the west coast of Novaya Zemlya.

The first four papers are grouped under the heading, "Scientific fishery investigations on the western Murman in the spring of 1929." In the first of these V. K. Yessipov describes his observations on the coastal cod fishery of the district. The most noteworthy find recorded is a rather extensive spawning of the cod which took place in May to such an extent that between the 5th and 7th May 31 % of the fish examined were found in a spawning condition[1]). The paper contains many interesting data on the size, weight and liver-content of the fish, also of the number of eggs counted in the roes of some specimens. The second paper, by V. K. Yessipov and E. S. Kutshina gives the result of scale readings. The figures quoted from their own research as to the age of the cod of different sizes compared with the results of other investigators (Suvorof, Hjort) shows sufficiently how uncertain and elusive is the use of cod scales, especially those from big fish. The size at different year-classes as found by the authors differs from that found by Hjort and Damas by up to 20 cm. (The only certain inference is therefore that age determination by means of scales is uncertain, to say the least.)

The third paper, by L. O. Retowskij and N. I. Tarassof, is an account, with tables, of the oceanographical conditions of the Motovski fjord during spring. Besides temperature and salinity observations at three points of this wide inlet and in some of the narrow branch fjords, a current measurement series of 26 hrs. in the central part of the fjord is recorded. (The diagrams of this, as well as in the rest of the collection, are too much reduced in size by the etcher to be easily legible).

The fourth paper is an account by N. I. Tarassof on the occurrence of pelagic cod, plaice and *Drepanopsetta* eggs in the Motovski fjord in the spring of 1929. The tables show that all three kinds of eggs were found fairly frequently in the fjord although only those of the cod in any numbers.

[1]) Ripe fish were found earlier in the spring at East Finmark. *O. S.*

The fifth paper by E. K. Suvorof and L. A. Vadova is a very interesting account (entirely in Russian) on the Barents Sea cod and haddock investigated on material provided by twenty experimental trawling expeditions from April 1927 to July 1928. The numbers of fish treated was, in all, about 9,500 cod and 1,500 haddock. The number for each voyage being in many cases under 50. It is therefore evident that the statistical value of this material can only be slight, although the comparison made in a series of curves between the sizes of cod in the Barents Sea and of the Norwegian catch at the same season during the Lofot and Finmark fisheries proves interesting, showing the sizes to be approximately the same at Finmark as farther east. The paper is marred by too great reduction of the figures and by several misprints in the tables.

The age is studied by means of scales, which are considered more trustworthy than admitted by the present writer (whose views are quoted) although inferior to fin ray grinds, which, however, involve too much work if great numbers of fish are to be treated. For haddock the scale method is considered to be more satisfactory than in the case of cod. The results are given in tables, which are rather crowded by hardly warranted decimals, and by graphs which require a lens to be studied. Tables are given of the relations of length and weight and of age and length of the two species as well as of the proportionate weight of the body, the head and the entrails of the fish.

The sixth paper, by E. Kutshina, refers to an investigation of the food of 513 cod of 3 to 101 cm. in length, caught at Portshinikha on the eastern Murman coast in 1928 and 1929. The omnivorous character of the cod is fully demonstrated by this painstaking analysis, which also shows a progressive change in predilections with increasing size.

The seventh paper, by A. Bazikalova, is a review of the parasitology of the Murman coast fishes.

The eighth paper is a translation of H. O. Bull's treatise on the state of maturity and chemical composition of the whiting, originally appearing in the Journal of the Marine Biological Association of the United Kingdom, Plymouth, 1928.

The ninth paper, by L. A. Vadova, is a study on the occurrence and growth of herring on the Murman coast in 1929—31, winding up with practical remarks on the salting or other treatment of small herring.

The tenth and eleventh papers, by V. K. Yessipov and G. S. Slastnikov, are short accounts of the characteristics of the Dab *(Pl. limanda)* and of the Rough Dab *(Drepanopsetta)* in the Barents Sea, with data on the catch in European waters. Both papers contain tables on the size and weight of the two fishes. Summaries are in German.

O. S.

G. F. Sleggs. "Observations upon the economic biology of the Caplin *(Mallotus villosus*, O. F. Müller)." Rep. Newfoundland. Fish. Res. Comm. Vol. 1, No. 3. Plymouth, 1933.

The author has succeeded in drawing up a useful and fairly complete account of the Caplin in Newfoundland waters, although the research work done for the purpose appears to have been collected in a more or less casual way, the author having admirably availed himself of all possible opportunities for observation and collection. Thus in each of the two years of observation, 1931 and 1932, records of first appearance were obtained from about 60 localities spread round the coasts, and from these

the conclusion is drawn that the annual migration is from deep water towards the adjacent land and not a progressive movement, e. g., from north to south. Temperature observations at the places visited by the caplin indicate an upper thermic limit of 10½° C. for the appearance of the shoals.

The question of the age of the fish is approached by means of a study of two samples of 3,468 and 4,245 individuals, the first of these being measured in 2 mm. groups and therefore giving a fairly smooth curve, while the other sample is measured in $^1/_8$-in. groups, resulting in a highly distorted curve from which the author, nevertheless, attempts to deduce the existence of modes representing 2 year-classes. By inference from the results of a study of the scales it is tentatively concluded that these two year-classes occurring as mature spawners are the 3-year-old fish, with a slight admixture of 2-year olds, while the one-year fish, which were obtained out at sea in May, seem to be represented by specimens of 5—8 cm. The spawning males were about 14 to 20 cm. long, the females 10.6—20, the latter being on the whole about 3 cm. smaller than the males. The study of the scales is well illustrated with drawings and photographs. The scales show at most two winter rings as scales are not present before the young fish have passed their first winter.

The spawning occurs near the shore down to 3 or 4 fathoms. The curious movements, known as "rolling", in the surf of dense swarms of the fish are described. By wave action the spawn is to a large extent concentrated in the intertidal zone where large quantities are destroyed by the maggots of a fly, *Fucellaria*. Indirect evidence goes to show the existence of spawning grounds in deep water also.

The sex ratio, although strongly fluctuating from sample to sample, seems to approximate to equality when counts over a long period are made. The occurrence of pelagic fry has been studied by a series of net hauls in all waters round the island, the greatest numbers being obtained near the northern extremity of the island and off Labrador. Hauls over greater depths than 100 fms. yielded no caplin fry.

In a final chapter much interesting information is collected regarding the use and value of caplin. An experiment of canning it at the Fisheries Research Laboratory is recorded as promising. The water-content has been determined in one sample as 80 % for the male fish and 87 % for the female, the oil content as 11 %.

The vitamin content in caplin oil is only slight, 3 % of the potency of cod liver oil for vitamin A while vitamin D seems to be absent or nearly so.

O. S.

M. Graham. "Report on the North Sea Cod." Min. of Agric. and Fish., Fish. Invest., Ser. II, Vol. XIII, No. 4, 1933. London, 1934.

Diese Arbeit enthält in gedrängter Darstellung die Bearbeitung eines sehr grossen Materials verschiedenster Herkunft und bezweckt eine möglichst vollständige Übersicht über die gesamte Biologie des Dorsches in der Nordsee.

Dies ist dem Verf. auch sehr wohl gelungen. Die Darstellung ist meistens fesselnd, oft geistreich, die Figuren verständlich (obwohl sie aber in vielen Fällen einen grösseren Masstab verdienten) und die Zahlenangaben nicht durch unnötige Stellen verschleiert.

Die Einleitung (mit der Vorsatzkarte) erwägt die relative Bedeutung der Dorschfischerei oder "Dorschdichte" in verschiedenen Gebieten. Es ergibt sich, dass die Nordsee eine mittlere Stellung einnimmt und 6 % des gesamten Dorschfanges der Welt liefert, 8 % des Nordseefanges aller

beteiligten Länder. Weitaus der grösste Anteil, 85 %, fällt auf Grossbritannien.

Teil 2 zeigt durch 7 vorbildliche Karten, wie stark gewohnheitsgebunden die Fischerfahrzeuge der verschiedenen britischen Häfen immer wieder dieselben Gebiete aufsuchen. 80 % der Anlandungen sind Schleppnetzfänge, davon entfällt fast die Hälfte auf Grimsby (60 von 149 tausend Tons in 1928). Die Sortierung in Marktsorten und deren Variationen wird eingehend besprochen.

Teil 3 enthält vorerst eine Erläuterung der für die Verwertung der Längenmessungen von Kleindorschen (Codling) verwendeten Methoden. Die Begründung für die Darstellung der Messungsreihen in 5 cm.-Klassen erscheint dem Ref. unzureichend. So zeigt 8, dass 2 cm.-Klassen vorzuziehen wären, wenn man sich nicht die Mühe einer Glättung nach der gewöhnlichen Formel $(a + 2b + c)/4$ leisten wollte, was ohne Zweifel viele interessante Einzelheiten aufgedeckt hätte. Die Methode ist jedoch völlig ausreichend um zu zeigen, dass das Wachstum der ersten drei Jahre in der Hauptsache nach zwei verschiedenen Modulen geht: rasches Wachstum südlich einer ungefähr von Hull nach NO. laufenden Linie, schwächeres nördlich derselben, so wie es H. Thompson auch für den Schellfisch gezeigt hat. Diese Linie folgt annähernd der Südgrenze des Gebiets, wo im Sommer eine Sprungschicht besteht, ferner der Tiefenzone 70—80 m. und der Bodenisotherme von etwa 8—10° C. Rascher Wuchs ist jedoch auch dem Moray Firth eigen.

Teil 4 behandelt die wichtigen Fragen: nachjugendliches Wachstum, Schätzung der Stärke der einzelnen Jahrgänge und deren Schwingungen.

Zuerst werden die am nächsten liegenden Hilfsmittel des Studiums dieser Fragen, die Schuppenuntersuchung und die Wachstumsdaten von wiedergefangenen markierten Fischen als unzulänglich für eine direkte und einfache Lösung abgelehnt, erstere wegen der Schwierigkeiten bei der Deutung der Schuppenbilder, letztere wegen der Spärlichkeit der Ergebnisse. Verf. war deshalb gezwungen, eine mehr indirekte Methode zu finden und zu benutzen, nämlich, kurz gesagt, eine rechnerische Lösung der durch mehrjähriges Messen von eigens dafür gemachten Fängen und von den Fängen der Berufs- (Schleppnetz-) Fischer gewonnenen monatlichen Grössenverteilungen.

Hierdurch werden die für jeden Monat wahrscheinlichen Durchschnittslängen jeder der 6 Jahresklassen, die den allerwesentlichsten Teil der Fänge ausmachen, bestimmt. Wenn diese Durchschnittslängen in demselben Diagramm des Wachstums mit den in direkterer Weise gewonnenen Längen der jüngsten Fische eingetragen werden (Abb. 19), ergibt sich ein auffallend stetiges Wachstum, ein Zeichen dafür, dass die Arbeitsmethode im wesentlichen sachgemäss gewesen ist und mit zureichender Umsicht durchgeführt wurde. Eine besondere Schwierigkeit bei der richtigen Berechnung der Modi der jüngsten Jahresklassen liegt in der Netz-Auslese, und diese Schwierigkeit, die natürlich von ausschlaggebender Wirkung für die weitere Berechnung wird, wird noch durch die grosse Verschiedenheit der von den Berufsfischern benutzten Netze erhöht. Die Erwägungen des Verf. in dieser Verbindung sind sehr lehrreich.

Für die Schätzung der Stärke der Jahrgänge wird besonders die Statistik (1905—14 und 1919—30) der Anlandungen von "kleinen" herangezogen und es wird auch gezeigt, wie diese Statistik für eine recht gute Voraussage der Fangmöglichkeit von kleineren Grössen von Jahr zu Jahr verwertet werden kann. Es zeigt sich, dass die stärksten Jahrgänge (1907 u. 1928) 12, bezw. 8-mal so zahlreich waren wie die schwächsten (1905, 1906, 1926).

Auf Grund aller Berechnungen und Erwägungen werden folgende Durchschnittslängen beim Abschluss jedes Wachstumsjahres angegeben: 18, 36, 55, 68, 78 und 89 cm.

Teil 5 gibt eine Übersicht des Lebenlaufes des Nordseedorsches.

Teil 6 behandelt eine Reihe allgemeiner Fragen wie Intensität der Fischerei in Verhältnis zum Bestand, Variationen und Identität des Bestandes, sowie die Möglichkeit der Voraussage der zukünftigen Dorschdichte. Der Verf. zeigt, dass der zu erwartende Fang von "grossen" auf Grund der Anlandungen von "kleinen" vor 3 und 4 Jahren sehr genau berechnet werden kann.

Die Wirkung der "Kriegs-Schonung" wird als eine Vermehrung der Zahl in der Sorte "gross" nachgewiesen, weil eine Steigerung der rel. Häufigkeit der *sehr* grossen Fische nicht stattfand.

Verf. lehnt den Gedanken ab, durch irgendwelche Schonmassnahmen den Bestand zu fördern um den Ertrag zu bessern, mit der Begründung, der Bestand sei nicht bedroht. Zur Frage der Bestandsfluktuationen durch etwaige gegenseitige Beeinflussung der Menge von Dorschen und deren Beutetieren bemerkt Verf., dass, obwohl Volterras Erwägungen über diesen Gegenstand richtig sein mögen, die von ihm aufgestellten Voraussetzungen für den Fall des Nordseedorsches nicht zutreffen.

Die Identität des Nordseebestandes wird unter Berücksichtigung des Stromsystems und der Markierungsergebnisse als ziemlich vollständig angesehen. Die nicht zu verleugnende Möglichkeit eines gelegentlichen Austausches mit benachbarten Gebieten (Skagerak, Norw. Küste) muss jedenfalls geringfügig sein.

Die 60 S. Tabellen enthalten sehr viel Interessantes. Die Zahl der zitierten Arbeiten ist 72. *Oscar Sund.*

F. S. Russell. "The Tunny, *Thunnus thynnus* Linnaeus." Science Progress. Vol. XXVIII, No. 112. London, 1934.

Biologists in general and ichthyologists in particular should be grateful to Mr. Russell for a paper in which is shortly collated, from a somewhat voluminous and confused mass of literature, a clear and readable account of the distribution and natural history of the tunny *(Thunnus thynnus* Linnaeus).

The following is a summary of the essential facts brought out in the paper reviewed — facts which, as Mr. Russell is at pains to point out, are not yet sufficiently amplified in many cases.

The egg of the tunny has been described as spherical, pelagic, 1.0 to 1.12 mm. in diameter, containing one large yellow oil globule 0.25 to 0.28 mm. in diameter, and as having a fine reticulated capsule and an homogeneous yolk. After a period of at most two days, there emerges a larva 3 mm long. No precise information of the subsequent development is yet to hand, nor is there similar information concerning the distribution of eggs and larval stages in any region.

Tunny born in June reach 300—500 g. in weight by September, and in their third year attain a weight of about 15 kg. and a length of nearly a metre. They are then probably mature.

The food of the adult fish appears to be that of the environment in which the fish finds itself, benthic fishes, squids and crustacea all having been found in their stomachs.

The spawning period for all regions in which tunny occur seems likely to be from the beginning of April until the last week in June, for in this

period mature fish are nowhere caught by hooks. Ripening and spent individuals are caught in certain localities, as they migrate in shoals to and from the place of spawning, by elaborate stake-net traps situated on the sea coast. The position of these traps or "madragues" in Tunis, Tripoli, Sardinia and Sicily and again on the Spanish, Portuguese and Moroccan coasts west of Gibraltar, infers spawning grounds somewhere between Sardinia, Sicily, and Tunis, and somewhere west of the Straits of Gibraltar. It is also thought that there may be another spawning ground near the Azores.

After spawning the tunny of the European side of the Atlantic embark on a feeding migration which may extend as far north as the Murman coast. With the onset of colder weather the area of distribution contracts to latitudes below those of British seas.

It is known that individual fish migrate between different regions of their distribution, but it is not known whether fish from different spawning areas remain generally true to that area or if there is a wider interchange.

The tunny occurs in the Mediterranean, the Black Sea, and in the eastern Atlantic from Morocco to the north of Norway.

Another species is found from Cape Hatteras to Nova Scotia, and on the Pacific coast of America there is a form which has also been established as a separate species — the "blue-fin tuna". Mr. Russell thinks it possible that these species are only subdivisions of the European one, but points out that *Thunnus orientalis* (Schlegels) — the common tunny of Japan — has been accorded separate specific status on good grounds.

R. S. W.

M. V. Lebour. "The Life-History of *Dromia vulgaris*." Proc. Zool. Soc. London. Pt. 2. London, 1934.

Although certain stages in the development of *Dromia* have long been known, Miss Lebour's account carries our knowledge forward considerably. She has obtained the first zoea by hatching from the egg, and the second and last stages from plankton, one specimen of the latter providing a megalopa by moult. She concludes that there are five stages in all. The special importance of the paper lies in its bearing upon the systematic position of the genus, which has generally been accepted as a member of the Brachyura or true Crabs. She shows that "the larvae differ in almost every point from those of the Brachyura." The zoea has a number of characters pointing on the one hand to relation to the Thalassinidea, and on the other to the Anomura, and she is doubtless right in her conclusion that "the Dromiacea must be removed from the Brachyura." How the true relationships are to be expressed is not so clear, for *Dromia* cannot be placed actually among the Anomura or the Thalassinidea. Miss Lebour's suggestion is that the Dromiacea should stand apart as a distinct group.

The life history of *Dromia* is an excellent example for those who urge that larval characters must be taken into account in framing systems of classification, and shows the danger of relying too much upon the general form of the adult. *Dromia* and some of its allies are so obviously "Crabs" in form that, in spite of such un-Crab-like features as the gill formula, they have readily been accepted as Brachyura. On the other hand the "Crab-facies" is known to have been independently assumed among the Anomura by *Lithodes, Porcellanopagurus* and *Porcellana,* and it seems now reasonably certain that *Dromia* is but another offshoot of the Anomuran stem, owing nothing to the Brachyura.

R. G.

Current Bibliography.

Prepared by the Editor with the assistance of Miss Thursby-Pelham.

NOTE. The scope of the Bibliography is limited in the main to the area covered by the Council's activities, but there are included papers of general interest relating to other areas in the North Temperate and Arctic regions and exceptionally elsewhere. Limnological references are not as a rule given, but papers relating to brackish waters and to salmon and freshwater fish studied by the Council are included.

The classification of entries follows in a general way that adopted in Dr. Allen's Selected Bibliography published in Vol. I, Nos. 1 and 2 of the Journal, and since reprinted (Price, 1 Kr.).

Subscribers and those on the distribution list will receive regularly upon application to the Administrative Secretary copies of the Bibliography printed on one side of the page only, for use in making up card indices.

The Editor will be glad to be advised of emendations and additions to the Bibliography.

Physical and Biological Conditions in the Sea.

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